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### A REVISION OF THE NORTH AMERICAN SPECIES OF *GENTIANELLA* MOENCH<sup>1,2</sup>

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When the genus *Gentianella* was segregated from the Linnaean *Gentiana* by Moench<sup>3</sup> in 1794 it contained but one species, *Gentianella tetrandra* Moench (= *Gentiana campestris* L.) one of the *amarella* group of gentians. In 1796 Borckhausen<sup>4</sup> published independently his own genus *Gentianella* to include the fringed gentians. These attempts at segregation were generally ignored, however, until 1894 when Kusnezow<sup>5</sup> brought together several of the present sections to constitute his subgenus *GENTIANELLA* of inclusive *Gentiana*, but without revision of the included species. Since then, only in occasional floras<sup>6</sup> has *Gentianella* been returned to generic rank with the name usually credited to Borckhausen rather than to Moench.

Thus the fundamental taxonomy of *Gentianella* has lain more or less dormant. It is astonishing that such showy and rather familiar plants should have been neglected until now. At the present time, particularly in the Americas, very few botanists even give recognition to the genus. This situation probably is due in part to the reluctance of taxonomists to undertake the many nomenclatural transfers required. Perhaps also there has been a tendency to avoid a genus with an obviously extreme degree of variability and with a range so wide that a regional study is difficult. Nevertheless this study, which includes but three of the possibly eight sections of the genus, has been attempted in an effort both better to indicate relationships and to bring order to the nomenclature.

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<sup>1</sup> Based on an investigation carried out in the graduate laboratory of the Henry Shaw School of Botany of Washington University and submitted as a thesis in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

<sup>2</sup> Contribution No. 1518, Botany and Plant Pathology Laboratory, Science Service, Canada Department of Agriculture, Ottawa, Ontario.

<sup>3</sup> Moench, C., Meth. Pl. 482. 1794.

<sup>4</sup> Borckhausen, M. B., in Roemer's Archiv für Botanik 1:23-32. 1796.

<sup>5</sup> Kusnezow, N. J., in Acta Hort. Petrop. 15:1-507. 1896-1904.

<sup>6</sup> cf. Schustler, Fr., in Vestnik Sjezdu Cesko Bot. v. Praze, 32-34. 1923.

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Although a natural classification ideally should be based on a study of a genus in its entirety, this is not always feasible. For practical reasons it has been necessary to select regions that provide abundant study material and opportunities to study the plants at first hand in the field. However, in order to maintain perspective, representative material for the remainder of the genus throughout its range has been examined where it has been readily available.

While *Gentianella* is not as large a genus as *Gentiana* (*sensu stricto*), nevertheless the total number of described species would have been unwieldy for the time available. Gilg, in his monograph,<sup>7</sup> described 182 South American species.<sup>8</sup> The number of species within the genus is not definitely established because many of those described still are included within *Gentiana*. Too often their descriptions are inadequate, so that a decision regarding their generic position is impossible without authentic material.

For this study nearly 4000 specimens have been examined from the major herbaria of North America and Europe. In addition, opportunity was afforded to study and to collect Canadian and northern United States species in the field.

This study has been based primarily on standard herbarium techniques and on field observations in natural habitats in the provinces of Alberta, British Columbia, Manitoba, Ontario, Quebec, Saskatchewan, in the Yukon Territory, and in the states of Idaho, Indiana and Wyoming. In general, seeds of North American material have been difficult to procure, and plants were difficult to maintain in cultivation. Seed exchange provides material frequently of dubious origin or consists primarily of European and Asian perennial species of *Gentiana*. More definitive studies of *Gentianella* in the future will require better facilities for observation under cultivation.

#### GENERIC POSITION

Gilg,<sup>9</sup> who made the most recent and comprehensive survey of the family, separated the Gentianaceae<sup>10</sup> into two subfamilies, the Gentianoideae and the Menyanthoideae. His key to the subfamilies and tribes is based primarily on pollen characters. The morphological and anatomical differences between these two subfamilies are evidently considerable as well, and although no phylogenetic relationship with other groups has been proposed it seems possible that these are two separate, perhaps scarcely related, families.

Gilg further divided his Gentianoideae into five tribes: the Gentianeae, Rusbyanthaeae, Helieae, Voyriaceae, and Leiphaimeae. The Gentianeae, in which we are primarily interested, he divided into the subtribes Exacinae, Erythraeinae, Chironiinae, Gentianinae and Tachiinae.

<sup>7</sup> Gilg, E., in Engler's Bot. Jahrb. 54 (Beibl. 118):4-89. 1916.

<sup>8</sup> Only one species of true *Gentiana* (*G. prostrata* Haenke) is recorded for the Andes.

<sup>9</sup> Gilg, E., in Engl. & Prantl, Nat. Pflanzenfam. ed. 1, 4<sup>2</sup>:50. 1895

<sup>10</sup> Dumortier, B. C., Analyse Fam. Pl. 20. 1829.

Within the subtribe Gentianinae, Gilg recognized seven genera: *Crawfordia*, *Jaeschkea*, *Gentiana* (*sensu lato*), *Ixanthus*, *Pleurogyne* (= *Lomatogonium*), *Swertia*, and *Halenia*. Since that time, as indicated in the historical survey which follows, *Crawfordia* has been united in part with *Gentiana* and in part with *Gentianella*.

*Gentianella* is more closely related to *Swertia*, *Lomatogonium*, and *Halenia* than to *Gentiana*. Two groups can clearly be distinguished on the basis of the position of nectaries: *Gentiana*, with glands at the base of the ovary; *Gentianella*, *Swertia*, *Lomatogonium*, and *Halenia*, with glands, foveae, or spurs borne on the surface of the corolla alternate with the stamens. The corolla of *Gentiana*, too, bears plicae or folds between the lobes, and the calyx has a membrane or rim extending completely around the interior of the tube. The calyx lobes, which arise from immediately below the edge of this membranaceous rim, may be foliaceous or they may be reduced to teeth. Kusnezow<sup>11</sup> has shown that this type of calyx has developed as an invagination of the inner epidermis of the tube. The intracalycular membrane is not consistently present in species of *Gentiana*; for example, *G. douglasiana* Bongard, a west-coast species, bears no membrane, but does exhibit corolla plicae accompanied by glands at the base of the ovary. In *Gentianella* and in the other three related genera, no such membrane exists. The small membrane that extends across the interior of the sinuses of the calyx in subgenus EUBLEPHIS (the fringed gentians) appears to be of different origin, for it is never continuous around the interior of the tube but is restricted to the sinus, and extends towards the center of the outer lobes only.

Again, in *Gentiana*, the corolla lobes have 3 principal vascular bundles, while in *Gentianella* there are 5-9. I have seen too few species of the other genera in the group to comment on this character. Borodin<sup>12</sup> reported calcium oxalate crystals in the leaf mesophyll of all the species of *Gentiana* (subgenus EUGENTIANA) that he examined but did not find them in the species of Kusnezow's subgenus GENTIANELLA.

Although not all species have been examined cytologically, and such information might shed new light on intergeneric and interspecific relationships, some broad evolutionary relationships may be discussed. It seems evident that *Gentiana* (*sensu stricto*), quite aside from its own complexity, forms part of a separate line of evolution. A second line comprises the genera *Gentianella*, *Halenia*, *Lomatogonium* and *Swertia*. These genera are rather closely related to one another through a development series of glands to foveae, foveae accompanied by squamellae and a development of the squamellae themselves, to the final development of spurs. It appears certain that *Halenia* originated from a *Swertia*-like ancestor, and differentiated by the development of spurs. Allen<sup>13</sup> is of the opinion that the foveate *Haleniae* are more primitive than the spurred ones, a point of view which seems

<sup>11</sup> Kusnezow, loc. cit. 1896-1904.

<sup>12</sup> Borodin, J., in Trav. Soc. Imp. Nat. St. Petersb. 22:131-137. 1892. (Russian).

<sup>13</sup> Allen, C., in Ann. Mo. Bot. Gard. 20:135. 1933.

reasonable. *Swertia* was shown by St. John<sup>14</sup> to be divisible into two groups, those bearing a single fovea on each petal, and those bearing two. In his revision, he used this difference as a major key character, although it appears to be of such prime importance as to suggest two separate evolutionary lines. *Lomatogonium* shows considerable affinity to *Swertia* because of the rotate corolla and the presence of squamellae.

Chromosome data available have contributed little towards the problem of generic delimitation. Table 1 provides calculated base numbers, gametic numbers, zygotic numbers and probable level of ploidy for a number of selected species.<sup>15,16,17</sup> From these data we glean that more than one series may exist within a genus; that the majority of the true gentians (genus *Gentiana*) of North America are diploids on a base of 13 (§ PNEUMONANTHE and § CHONDROPHYLLA), that the European § APTERA has base numbers of 7 and 13, that the Old World § THYLACITES has a base of 9, and that § CYCLOSTIGMA has a base of 7; that the genus *Gentianella* has a base 9 in both series AMARELLA and series ARCTOPHILAE of § AMARELLA, and that subgenus EUBLEPHIS (= § CROSSOPETALUM) has two series each of 11 and 13. The diploid subgenus COMASTOMA has a base of 5 in common with the genus *Lomatogonium*.

<sup>14</sup> St. John, H., in Amer. Midl. Nat. 26:1-29. 1941.

<sup>15</sup> Rork, C., in Amer. Jour. Bot. 36:687-701. 1949.

<sup>16</sup> Favarger, C., in Bull. Soc. Bot. Suisse 59:62-86. 1949; 62:244-257. 1952.

<sup>17</sup> Löve, D., in Hereditas 39:225-235. 1953.

TABLE I\*

	Calculated base number	Gametic number	Zygotic number	Probable level of ploidy	Author and year
<i>Gentiana</i>					
COELANTHE					
<i>G. lutea</i>	5 or 7	ca. 17-18			Woycicki, 1935
		21	42		Stolt, 1921
		20	40		Favarger, 1949, 1952
<i>G. purpurea</i>	5	20			Favarger, 1949
PNEUMONANTHE					
<i>G. andrewsii</i>	13	13	26	Dipl.	Rork, 1949
<i>G. asclepiadea</i>	11	22		Dipl.	Favarger, 1949
			44		Rork, 1949
<i>G. cherokeensis</i>	13	13	26	Dipl.	Rork, 1949
<i>G. clausa</i>	13	13	26	Dipl.	Rork, 1949
<i>G. decora</i>	13	13	26	Dipl.	Rork, 1949
<i>G. gebleri</i>	13	13		Dipl.	Sokolovskaja & Strelkova, 1938
<i>G. linearis</i>	13	13	26	Dipl.	Rork, 1949
<i>G. makinoi</i>	13		26	Dipl.	Sakai, 1934
<i>G. pneumonanthe</i>	13	13		Dipl.	Scheerer, 1939
<i>G. porphyrio</i>	13	13	26	Dipl.	Rork, 1949
<i>G. puberula</i>	13	13		Dipl.	Rork, 1949
<i>G. saponaria</i>	13	13	26	Dipl.	Rork, 1949
<i>G. villosa</i>	13	13	26	Dipl.	Rork, 1949
FRIGIDA					
<i>G. frigida</i>	13	13		Dipl.	Sokol. & Strel., 1938

TABLE I (Continued)

	Calculated base number	Gametic number	Zygotic number	Probable level of ploidy	Author and year
APTERA					
<i>G. cruciata</i>	13	26	52	Tetra.	Favarger, 1949 Rork, 1949
<i>G. daburica</i>	13	13	26	Dipl.	Rork, 1949
<i>G. gracilipes</i>	13	13	26	Dipl.	Rork, 1949
<i>G. macrophylla</i>	7	21	42	Hexa.	Rork, 1949
<i>G. phlogifolia</i>	13		52	Tetra.	Rork, 1949
<i>G. straminea</i>	13		52	Tetra.	Rork, 1949
CHONDROPHYLLA					
<i>G. altaica</i>	13	13			Sokol. & Strel., 1938
THYLACITES					
<i>G. acaulis</i>	9		36	Tetra.	Rork, 1949
<i>G. alpina</i>	9	18		Tetra.	Favarger, 1949
<i>G. clusii</i>	9	18		Tetra.	Favarger, 1949
<i>G. kochiana</i>	9	18		Tetra.	Favarger, 1949
CYCLOSTIGMA					
<i>G. nivalis</i>	7	7		Dipl.	Favarger, 1949
<i>G. verna</i>	7	14		Tetra.	Favarger, 1949
<i>Gentianella</i>					
subg. GENTIANELLA					
sect. AMARELLA					
ser. AMARELLAE					
<i>G. amarella</i>	9		36	Tetra.	Favarger, 1949, 1952 Skalinska, 1952 Löve, 1953
<i>G. campestris</i>	9	18	36	Tetra.	Favarger, 1949 Löve, 1953
ser. ARCTOPHILAE					
<i>G. aurea</i>	9		36	Tetra.	Rork, 1946; Löve, 1953
<i>G. quinquefolia</i>	9	18	36	Tetra.	Rork, 1949
subg. EUBLEPHIS					
<i>G. ciliata</i>	11	22		Tetra.	Favarger, 1949
<i>G. detonsa</i>	11		44	Tetra.	Löve, 1953
<i>G. crinita</i>	13		78	Hexa.	Rork, 1949
<i>G. procera</i>	13	39			Rork, 1949 Denniston, 1913
subg. COMASTOMA					
<i>G. tenella</i>	5		10	Dipl.	Favarger, 1949 Knaben, 1950 Löve, 1953
<i>Lomatogonium</i>					
<i>L. rotatum</i>	5	5	10	Dipl.	Löve, 1953
<i>Swertia</i>					
<i>S. cuspidata</i>	9		18		Sakai, 1940 Woycicki, 1937
<i>S. perennis</i>		12			
<i>Frasera</i>					
<i>F. caroliniensis</i>	13	39	78	Hexa.	Rork, 1949

\* Interpretation of the level of ploidy is, in many cases, that of the author. For more complete information see the references cited.

Tetraploidy seems to be the rule in North American subgenus *GENTIANELLA*, and tetraploidy and hexaploidy the rule in subgenus *EUBLEPHIS*. The diploid subgenus *COMASTOMA* is left provisionally in *Gentianella*. Of the seventy or more genera of Gentianaceae only the herbaceous members of the north temperate zone seem to have been investigated cytologically and these in a general manner only; i.e., selected species rather than all species. Probably investigations have been dependent upon the availability of seed.

*Gentiana*, then should be restricted to include those plants with glands at the base of the ovary and plicae between the lobes of the corolla, whether or not an intracalycular membrane is present. *Halenia*, with its spurs and dextrorse convolution of the corolla lobes in the bud, is evidently closely related to *Gentianella* subgenus *GENTIANELLA*.

Late-flowering plants of *Halenia deflexa* occasionally form spurless flowers that are nearly indistinguishable from *Gentianella amarella*. Nevertheless, in spite of these occasional irregularities, *Halenia* appears to be quite a distinct group worthy of generic rank. Subgenus *EUBLEPHIS* of *Gentianella*, on the other hand, while distinct from subgenus *GENTIANELLA* in ovule arrangement, constant tetramery, calyx formation, papillose seeds, etc., has been retained at the subgeneric rank to indicate close relationship with the amarellas and for reasons of usage.

I should again emphasize that this study of the North American species of *Gentianella* includes but three of the eight sections assigned to this genus (other sections include: *DASYSTEPHANA* Griseb. (not Adans.), *ANDICOLA* Griseb., *IMAI-COLA* Griseb., *ANTARCTOPHILA* Griseb., and *PTERYGOCALYX* Maxim.), and but a minor number of the total species involved.

The segregation of *Gentianella* roughly divides the gentians into two phylogenetically distinct and quite convenient units. To separate further the fringed group as did Yu-chuan Ma,<sup>18</sup> chiefly on the ovule arrangement, sets a precedent that might make it necessary at a later date to segregate sections of *Gentiana* on this character. Finally we should achieve a larger number of segregates, a larger number of nomenclatural changes, and add very little more to an understanding of the group. This understanding can best be expressed by raising or lowering the ranks of the sections without unduly disturbing the generic concepts. Within *Gentianella* it is sufficient to show that the fringed gentians are distinct from the amarellas but no more so than is *G. tenella*, and that the amarellas and arctophilas are far more closely related.

In order to illustrate the position of *Gentianella* with respect to the other genera of the Gentianinae, I have prepared a key to the genera of the subtribe, including the genus *Megacodon* H. Smith of which unfortunately no material was available to me. In this instance characters employed in the key are taken from Hemsley's original description and from his extremely fine plate.

<sup>18</sup> Ma, Yu-chuan, in *Acta Phytotax.* 1:1-19. 1951

## KEY TO THE GENERA OF THE GENTIANINAE

- a. Whorl of nectary glands at the base of the ovary, never appearing upon the base of the corolla tube.
- b. Corolla without interlobal plicae; calyx tubular without an intracalycular membrane, or the sepals free.
- c. Ovary approaching a bilocular condition by a lamellate intrusion of the placentae into the locular cavity; sepals united.....*Ixanthus*
- cc. Ovary unilocular, the ovules restricted to the sutures and with an additional row between them; sepals free.....*Megacodon*
- bb. Corolla with interlobal plicae; calyx tubular, generally with an intracalycular membrane, or spatheform.....*Gentiana*
- aa. Whorl of nectaries upon the base of the corolla tube alternate with the stamens.
- d. Corolla tube spurred, foveate, or fimbriate at the base.
- e. Stigmas decurrent along the carpel sutures.....*Lomatogonium*
- ee. Stigmas terminal.
- f. Corolla lobes sinistrorsely convolute in the bud, spurless, with one or two fimbriate foveae at the base of the corolla tube.....*Swertia*<sup>19</sup>
- ff. Corolla lobes dextrorsely convolute in the bud, each with a non-fimbriate spur at the base of the corolla tube, or rarely spurless.....*Halenia*
- dd. Corolla tube bearing glands at the base between the stamens, never spurred, foveate, nor fimbriate at the base.
- g. Stamens inserted at the middle of the corolla tube or below; corolla imbricate in the bud; seeds generally many in each capsule.....*Gentianella*
- gg. Stamens inserted at the sinus of the corolla lobes; corolla valvate in the bud; seeds few in each capsule.....*Jaeschkea*

## HISTORICAL SURVEY

The genus *Gentianella* is a segregate of the much larger *Gentiana*; hence their histories are closely interwoven. Although rather well treated by Kusnezow<sup>20</sup> in the monograph of his subgenus EUGENTIANA, a review of the history up to modern times and with stress on that of *Gentianella* will assist in an understanding of the generic problems existing in this portion of the Gentianaceae today.

*Gentiana* is generally accredited to Tournefort<sup>21</sup> who used a Dioscoridean<sup>22</sup> name commemorating legendary King Gentius of Illyria. Rupprius<sup>23</sup> recognized two genera, *Gentiana* and *Gentianella*, both of which are included within the modern *Gentiana* (*sensu lato*). In his 'Genera Plantarum' of 1737, Linnaeus took up Tournefort's *Gentiana*, dividing the genus into seven groups, some of which correspond to contemporary sections. Later, in his 'Species Plantarum' of 1753, he redivided *Gentiana* less successfully into three groups as follows:

1. \**Corollis quinquefidis subcampaniformibus* [includes *G. lutea*, *G. purpurea*, *G. punctata*, *G. asclepiadea*, *G. pneumonanthe*, *G. saponaria*, *G. villosa*, *G. acaulis*].
2. \*\**Corollis quinquefidis infundibuliformibus* [includes *G. verna*, *G. bavarica*, *G. nivalis*, *G. aquatica*, *G. utriculosa*, *G. centauria*, *G. spicata*, *G. quinquefolia*, *G. amarella*].
3. \*\*\**Corollis non quinquefidis* [includes *G. campestris*, *G. ciliata*, *G. cruciata*, *G. sessilis*, *G. filiformis*, *G. perfoliata*].

<sup>19</sup> No attempt is made here to distinguish between *Swertia* and *Frasera*.

<sup>20</sup> Kusnezow, loc. cit. 1896-1904.

<sup>21</sup> Tournefort, J. P., Inst. Rei Herb. 80. t. 40. 1700.

<sup>22</sup> Gunther, R. T., The Greek Herbal of Dioscorides. Oxford, 1934.

<sup>23</sup> Rupprius, H. B., Fl. Jen. ed. 2. 17. 1726; ed. Hall. 21. 1745.

Necker,<sup>24</sup> in 1790, included most of the Gentianoideae in one of his all-inclusive "genera". His "genus" *Darinyphytum* not only included most of the Gentianoideae but also a great variety of incongruous groups from a number of modern families. Within this "genus" he recognized a number of "species". Some of these, "*Pneumonantbe*", "*Anthopogon*", "*Spiragyne*", and "*Thyrophora*", are equivalent in extent to modern genera. In most cases his descriptions are so inadequate that these "species" cannot be identified readily with modern taxa. Plates published in his 'Elementa Botanica' demonstrate characters used in the diagnosis of his super-genera.

This ambiguity of description, failure to include names on which his "species" were based, and his usage of a species concept quite at variance with either modern practice or that of other authors of his day, make these names *nomina invalida*. Significantly, perusal of the 1950 International Code reveals that fifty-seven Neckerian names have been rejected for one reason or another, against six conserved and three proposed for conservation.

In 1794, Moench<sup>25</sup> described the genus *Gentianella*, basing it on *Gentiana campestris* L. which he renamed *Gentianella tetrandra*. No other species were assigned by him to the genus.

In 1796, Schmidt<sup>26</sup> divided *Gentiana* of Linnaeus into six segregate genera: *Pneumonantbe*, *Hippion*, *Chironia*, *Gentiana*, *Swertia* and *Chlora*. *Hippion* included sections CROSSOPETALUM Froelich, AMARELLA Griseb. and ARCTOPHILA Griseb., now included within *Gentianella*. Borckhausen,<sup>27</sup> in a paper following in the same publication, divided Linnaeus' genus into thirteen genera of which *Gentianella* corresponded to section CROSSOPETALUM of Froelich.

Froelich<sup>28</sup> monographed *Gentiana*, also in 1796, describing 47 species which he divided into four undenominated groups: COELANTHE, CALATHIANAE, ENDOTRICHAE, and CROSSOPETALAE. Many later authors have assumed these to be sections. In 1829, Bunge<sup>29</sup> described 80 species of *Gentiana* but maintained a classification somewhat influenced by Borckhausen. His section CROSSOPETALAE corresponded to Grisebach's CROSSOPETALUM. Endlicher<sup>30</sup> essentially adopted Bunge's system in his 'Genera Plantarum' and maintained section CROSSOPETALUM Froel.

Grisebach's monographic study of the Gentianaceae<sup>31</sup> is one of the landmark works of the family. His genus *Gentiana* contains some 125 species, which are divided into seven sections. In his treatment of the Gentianaceae in De Candolle's 'Prodromus' in 1845,<sup>32</sup> the number of species was increased to 153. In 1838 the

<sup>24</sup> Necker, N. J., Elem. Bot. 2:11-14. 1790.

<sup>25</sup> Moench, loc. cit. 482. 1794.

<sup>26</sup> Schmidt, F. W., in Roemer's Archiv f. Bot. 1:3-23. 1796.

<sup>27</sup> Borckhausen, loc. cit. 1796.

<sup>28</sup> Froelich, J. A., Gent. Diss. 1796.

<sup>29</sup> Bunge, A., in Nouv. Mem. Soc. Imp. Nat. Moscou 1:197-256. 1829.

<sup>30</sup> Endlicher, S. L., Gen. Pl. 600. 1836-40.

<sup>31</sup> Grisebach, A. H. R., Gen. et Spec. Gent. 1839.

<sup>32</sup> DC. Prodr. 9:86-119. 1845.



North American species were treated separately by Grisebach in Hooker's 'Flora Boreali-Americana'.<sup>33</sup>

Huxley<sup>34</sup> in 1888 suggested a rearrangement of the family based on the position of the corolla glands. His MESOMELITAE includes the plants having glands at the base of the ovary, while his PERIMELITAE includes those with epipetalous glands. In 1860, Turczaninow<sup>35</sup> monographed *Gentiana* in his 'Monographische Beschreibung der Enzianen'.

In 1892, Murbeck<sup>36</sup> published a small study of the European ENDOTRICHAE which includes several new species with distribution maps of some entities. He failed to include keys to the species.

In 1894, Kusnezow<sup>37</sup> divided the Linnaean genus into two subgenera, EUGENTIANA and GENTIANELLA. His voluminous monograph covers his subgenus EUGENTIANA only. He made no attempt to revise subgenus GENTIANELLA beyond establishing characters to distinguish it. This monograph was later translated from the Russian into German and was published in parts from 1896 to 1904. Kusnezow<sup>38</sup> again maintained the subgenus GENTIANELLA in his treatment in Engler and Prantl's 'Die Natürlichen Pflanzenfamilien' in 1895.

In 1896, Wettstein<sup>39</sup> monographed the European species of the section ENDOTRICHIA, recognizing 27 species; and in 1900, he revised the North American species of the same section.<sup>40</sup> In 1896, Wettstein<sup>41</sup> segregated *Gentiana tenella* Rottb. from the section ENDOTRICHIA, erecting a new section COMASTOMA.

In 1901, Th. Holm<sup>42</sup> presented a short revision of the Canadian species of the section CROSSOPETALUM of which he described three new species.

In 1917, Gilg<sup>43</sup> monographed the South American species of *Gentiana*, recognizing 182 species of subgenus GENTIANELLA and one species of the subgenus EUGENTIANA. In this work he created a series of divisions to which he assigned no rank.

Schustler<sup>44</sup> returned *Gentianella* to the rank of genus in 1923, incorrectly ascribing it to Borckhausen rather than to Moench.

In 1936, H. Smith<sup>45</sup> raised Hemsley's section MEGACODON of *Gentiana* to the rank of genus, and in 1937, Marquand<sup>46</sup> united the genus *Crawfurdia* to *Gentiana*, but relegated the section PTERYGOCALYX Maxim. of *Crawfurdia* to *Gentian-*

<sup>33</sup> Hooker, W. J., Fl. Bor-Amer. 2:54. 1838.

<sup>34</sup> Huxley, T. H., in Jour. Linn. Soc. Bot. 24:101-124. 1888.

<sup>35</sup> Turczaninow, N., in Nat. Sci. Meetings, 34-35. 1860 (Not seen).

<sup>36</sup> Murbeck, Sv., in Acta Hort. Berg. 2<sup>3</sup>:1-28. 1892.

<sup>37</sup> Kusnezow, loc. cit. 1896-1904 (German; Russian ed. 1894, not seen).

<sup>38</sup> Nat. Pflanzenfam. ed. 1, 4<sup>2</sup>:85. 1895.

<sup>39</sup> Wettstein, R. V., in Denkschr. K. Akad. Wiss. Wien, math.-nat. Cl. 64:1-73. 1896.

<sup>40</sup> Oesterr. Bot. Zeitschr. 50:168-173, 189-195, 290-293. 1900.

<sup>41</sup> Oesterr. Bot. Zeitschr. 46:121-128. 1896.

<sup>42</sup> Ottawa Nat. 15:175-183. 1901.

<sup>43</sup> loc. cit. 1917.

<sup>44</sup> loc. cit. 1923.

<sup>45</sup> Smith, Harald, in Handel-Mazzetti, Symb. Sin. 7:950. 1936.

<sup>46</sup> Marquand, C. V. B., in Kew Bull. 134-180. 1937.

*ella*. In an earlier paper<sup>47</sup> he had merely excluded PTERYGOCALYX from *Gentiana*.

Yu-chuan Ma,<sup>48</sup> in 1951, raised the section CROSSOPETALUM to generic rank, naming the genus *Gentianopsis*, but discussed no synonymy. However, whether by design or accident, no earlier generic name would have been valid for this group.

#### GENERAL MORPHOLOGY

The North American species of *Gentianella* are glabrous herbs. In habit the plants are branched or simple. Of the North American species, only *G. barbellata* is a true perennial; the others are either annual, biennial or perhaps winter annuals. Actual growth tests are needed to determine their life cycle.

The primary root is rather small in comparison with the size of the entire plant and is slightly thickened, forming a slender tap-root. As a rule there are few secondary roots. In *G. barbellata* there is a horizontal rhizome which apparently grows a few inches below the surface of the soil and sends vertical branches upward to the surface. At the surface level these branches thicken considerably and are enveloped in the basal rosette. These horizontal rhizomes seldom are collected and appear on only the occasional dried specimen. Probably collectors as a rule do not take the trouble to dig into the stony ground of alpine tundras!

The stems frequently become woody at the base and, in coarse plants such as *G. crinita*, they become hollow in the lower part. Various developed stem-wings occur in many of the plants, or the stems may be prominently angled or striate. The wings, however, vary to such a degree that the character is of little diagnostic value. In some plants the wings are twisted spirally about the lower part of the stem. This feature greatly influences the symmetry of the phyllotaxy, so that the leaves, instead of being strictly decussate, show a distinct shift in their position at each successive node.

The leaves in *Gentianella* are glabrous as are those of the entire family. Basal leaves are spatulate to lingulate, and may be sessile or the blade may be attenuated rather sharply to a narrow, decurrent, connate, or clasping petiole. These leaves may wither early in the season. The shape of the median leaves is sufficiently diagnostic to be useful as a supporting character. In the fringed gentians the leaves usually have a single mid-vein; in the amarellas, arctophilas and comastomas the venation is palmate with three to five nearly parallel veinlets. The mid-vein is generally fairly prominent, while the laterals may or may not be distinct. Leaf margins are entire throughout the genus, occasionally minutely papillose or ciliate under magnification.

If a leaf be carefully pulled downwards and torn from the stem so that a fragment of the stem epidermis is removed with it, several minute processes or squamel-

<sup>47</sup> Kew Bull. 66-68. 1931.

<sup>48</sup> loc. cit. 1951.

lae may be found attached to the base. These structures have been reported in other families of the Contortae, and may represent reduced stipules.<sup>49</sup>

The inflorescence is basically cymose, consisting of a simple cyme, an aggregate umbelliform cyme borne in a compact head, or may be reduced to a single terminal flower on a slender pedicel. Often flowers are borne singly or in pairs in the axils of the cauline leaves (dichasium). The upper leaves may frequently become bract-like and envelop the inflorescence, as in *G. aurea*.

The calyx is tubular in all species except *G. wislizeni* where the tube is split down one side to form a spathe, with the lobes reduced to minute teeth at the apical margin. Grossheim<sup>50</sup> described this condition for the European *G. ciliata* but I have never seen this type of calyx in any of the North American fringed gentians.

In subgenus EUBLEPHIS (the fringed gentians) there are four calyx lobes, probably representing an inner and an outer cycle. The lobes of this group are thinly membranaceous, usually hyaline-margined, the outer lobes frequently plicate and carinate at the tip. The sinuses of the calyx lobes have a small internal hyaline membrane which bears a row of minute blunt processes. The venation of the lobes of subgenus EUBLEPHIS is usually reticulate.

In subgenera GENTIANELLA and COMASTOMA there may be four calyx lobes or five forming a quincunx. The lobes vary in shape and length with respect to the tube and furnish useful characters. The calyx lobes of these two subgenera are somewhat fleshy. A mid-vein and two lateral veins occur and the laterals either unite below the sinus or at the base of the tube. Squamellae are usually found on the inner surface of the calyx tube near the base. These structures, however, are of little taxonomic value.

The corolla may be tubular, funnelform, or salverform when the lobes are fully expanded. In North American species its color varies from white to yellow, blue, and violet. South American species are often brilliant yellow or red. The lobes are oblong, obovate, ovate, to triangular, with acute, apiculate, mucronate, or obtuse tips. At the base of the lobes in many species there is a horizontal row of fimbriae (the crown) which may be free or may be united at the base to form a fringed scale. In section AMARELLA these fimbriae usually are continuous across the base of the lobe, sometimes irregularly scattered, with a vascular trace in each fimbria. In the COMASTOMAE, on the other hand, there are two separate fimbriate scales at the base of each corolla lobe and there are no vascular strands within the fimbriae. As in certain apocynaceous corollas, these scales may be of stipular origin.<sup>51</sup>

At the base of the corolla tube and alternate with the stamens are small glands or nectaries of various shapes. These never appear foveate, but are more frequently swollen. The glands are never accompanied by fimbriae.

<sup>49</sup> Holm, R. W., in Ann. Mo. Bot. Gard. 37:484. 1950.

<sup>50</sup> Grossheim, A. A., in Fl. U. S. S. R. 18:591. 1952.

<sup>51</sup> Woodson, R. E. & Moore, J. A., in Bull. Torr. Bot. Club 65:135-165. 1938.

The stamens are equal in number to the corolla lobes and are alternate with them. Occasionally in *G. wislizeni* and *G. microcalyx* the anthers abort, with the staminodia elongate or reduced to small protuberances. The stamens are inserted near the center of the tube or below. The filaments usually are winged at the base, the wings curving inwards to form a canaliculate filament. The anthers are oblongoid or ovoid, and versatile, appearing introrse before dehiscence, then rotating and becoming extrorse following dehiscence. The three-pored pollen grains are essentially uniform in the genus.

The size and shape of the pistil are dependent upon the age of the flower. Prior to fertilization the style frequently is distinct; after fertilization it may gradually disappear with the maturation of the ovary and the formation of the capsule. The gynophore may also vary in length and distinctness with age. In some species the pistil is sessile or subsessile; in others the gynophore may be minute in young flowers, elongating considerably as the capsule matures. In some the gynophore always is elongate.

The two stigmas vary considerably in size and shape. They may be flabelliform and broad; or oblong, elliptic, or reniform and narrow. Their margins may be entire, sinuous or toothed—all features that vary within a population.

Seeds are of very great value to distinguish sections, but in most instances fail to separate species. Those of subgenus EUBLEPHIS are oblong and frequently angular, with reticulate or papillose surfaces. In two species, however, *G. simplex* and *G. ciliata* of Europe, they are reticulate and pronouncedly caudate. Those of subgenus GENTIANELLA series AMARELLAE and ARCTOPHILAE, as well as those of subgenus COMASTOMA, are round to slightly flattened. The color almost invariably is light brown.

#### GEOGRAPHICAL DISTRIBUTION

The genus *Gentianella* has an almost global distribution. In North America the two subgenera EUBLEPHIS and GENTIANELLA, have roughly a similar distribution but apparently different histories. Both groups have species that occur in Europe and Asia and connect with North America through either Greenland or Alaska. The variability and complexity found in the North American populations also occur in Asia and Europe. The South American species of the genus are placed chiefly in sections IMAICOLA and ANDICOLA.

In subgenus COMASTOMA only one widespread species, *G. tenella*, is represented in North America. This species occurs in Colorado south to Arizona and New Mexico, west to California, and in a few scattered stations across Alaska, Canada, and Greenland. The same species is common in Iceland, northern Europe and in the high mountains of southern Europe and Asia.

The fringed gentians (EUBLEPHIS) exhibit interesting distributional patterns. *G. simplex* and *G. barbellata* both occupy rather limited areas below the margin of maximum glaciation and probably have had quite an independent and

an older history than the *detonsa-crinita* complex. The seed of *G. simplex* of California bears a striking resemblance to that of *G. ciliata* of Europe. This seed similarity between these two species prompted Engelmann<sup>52</sup> to set up two groups or series of undesignated rank to indicate this relationship: a. Lepidospermae (*G. crinita*, *G. lanceolata*, *G. barbellata*), b. Pterospermae (*G. ciliata*, *G. simplex*). Seed similarity is the only major character that these two species have in common, so the classification of Engelmann may not represent true relationships. Recently Grossheim in the 'U.S.S.R. Flora' employed a similar division of the species (Series CILIATAE and BARBATAE) but based it on floral characters, apparently failing to note the distinct nature of the seed of *G. ciliata*.

If we hypothesize a Eurasian origin, there may have been several "invasions" of the *detonsa-crinita* complex into North America. The meagre, but no less valuable, chromosome data at hand indicate an  $n = 13$  series represented by *G. crinita* and its ssp. *procera*, and an  $n = 11$  series represented by *G. detonsa* (probably ssp. *detonsa*), hexaploid and tetraploid species respectively. The most stable portion of the complex is that occurring south of glaciation. Apparently the *crinita* group entered North America either from the north and reached the Appalachians, or arose independently there. The *detonsa* group perhaps entered through Alaska and migrated southwards as far as central Mexico with a branch into California (ssp. *holopetala*). Glaciation probably eradicated the group in the north except for a few isolated refugia. This may have been followed by a remigration back into the deglaciated area from Alaska-Yukon by means of the Yukon and Mackenzie River systems. The southern portion of the *detonsa* population was unable to move north perhaps through lack of suitable high altitude/high latitude habitat requirements. The *crinita* group, finding suitable low altitude/low latitude habitats, moved rapidly northwestward into the Great Lakes region and across the plains as far as the Rocky Mountains to close the population gap.

This broad conjectural outline may aid in understanding the subspecific treatment afforded this complex. The various populations are more or less imbricate in their distribution—or in the case of the *crinita* group, clinal—indicating a differentiating process accompanying the migration flow. Further discussion follows in the taxonomic treatment.

#### STUDY MATERIAL

Specimens or photographs from the following institutions have been available for the purpose of this study, either through loans or by visits to the herbaria. For

<sup>52</sup> Engelmann, G., in Trans. Acad. Sci. St. Louis 2:216. 1868.

the sake of consistency, the abbreviations used are those listed by Lanjouw and Stafleu.<sup>53</sup>

- A—Arnold Arboretum, Cambridge, Mass.  
 C—Universitets Botaniske Museum, Copenhagen, Denmark.  
 CAN—National Museum of Canada, Ottawa, Ont.  
 DAO—Botany and Plant Pathology Laboratory, Science Service, Canada Department of Agriculture, Ottawa, Ont.  
 F—Chicago Natural History Museum, Chicago, Ill.  
 GH—Harvard University Herbarium, Cambridge, Mass.  
 ID—Herbarium of the University of Idaho, Moscow, Ida. (This includes the Botany Herbarium and the Range Herbarium of the Department of Forestry).  
 JBM—Jardin Botanique de Montréal, Montréal, P. Q.  
 MEXU—Herbario Nacional del Instituto de Biología de la Universidad Nacional de México, Mexico, D. F.  
 MO—Missouri Botanical Garden, St. Louis, Mo.  
 MIN—Herbarium, University of Minnesota, Minneapolis, Minn.  
 NY—New York Botanical Garden, New York, N. Y.  
 ND—Herbarium, University of Notre Dame (Greene-Nieuwland Herbarium), Notre Dame, Ind.  
 PH—Academy of Natural Sciences, Philadelphia, Pa.  
 S—Naturhistoriska Riksmuseum, Stockholm, Sweden.  
 SWC—Dominion Experimental Station, Swift Current, Sask.  
 UBC—University of British Columbia, Vancouver, B. C.  
 UC—Herbarium of the University of California, Berkeley, Calif.  
 US—United States National Herbarium, Washington, D. C.  
 WS—State College of Washington, Pullman, Wash.  
 RM—Rocky Mountain Herbarium, University of Wyoming, Laramie, Wyo.

*Citation of Specimens:* For reasons of economy, citations have been considerably reduced. Specimens of species represented by little material have been cited in full. Those of common and widely distributed species have been reduced. One specimen from each county or, lacking counties, places or districts is cited. Individual collections have been selected for citation on the basis of breadth of distribution of duplicates or of historical importance.

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#### TAXONOMIC TREATMENT

GENTIANELLA Moench, Meth. Pl. 482. 1794, emend. Schustler, in Vestnik Sjezdu Cesko Bot. v. Praze, 32–34. 1923. (T.: *Gentianella tetrandra* Moench based on *Gentiana campestris* L. Sp. Pl. ed. 1, 231. 1753 = *Gentianella campestris* (L.) Börner, Fl. deut. Volk, 543. 1912.)

<sup>53</sup> Lanjouw, J., and Stafleu, F. A., in *Regnum Vegetabile 2. Index Herbariorum*, p. 131. ed. 2, 1954.

*Anthopogon* Necker, Elem. Bot. 2:12. 1790, ut species; Raf. Fl. Tellur. 3:25. 1837, ut genus, non Nutt. Gen. N. Amer. Pl. 1:81. 1818.

*Spiragyne* Neck. loc. cit. 12. 1790, ut spec., nom. ambig.

*Opsantha* Delarb. Fl. d'Auvergne, ed. 2, 30. 1800.

*Gentiana* L. subg. *Gentianella* Kusnez. in Engler & Prantl, Nat. Pflanzenfam. ed. 1, 4<sup>2</sup>:85. 1895.

Caulescent or acaulescent annual, biennial, winter annual, or perennial herbs, rarely shrubs (in South America), usually with tap-roots, rarely with slender rhizomes. Leaves opposite, membranaceous or fleshy, sessile or petiolate, usually palmately 3- to 5-veined, the veins prominent or inconspicuous. Inflorescence a terminal or axillary umbelliform dichasium, or an aggregate or simple cyme, frequently 1-flowered. Calyx 4- to 5-lobed, tubular, obconic, or 4-angulate, rarely spathiform, without an inner continuous membranaceous rim, carinate or ecarinate, glabrous or scabrous-papillose, frequently bearing a number of minute squamellae within and at the base of the tube. Corolla 4- or 5-lobed, marcescent, tubular, funnel-form, campanulate, to rotate (in S. American species), the tube with or without faucal fimbriae; lobes with 5-9 parallel veins, sinistrally or quincuncially convolute in the bud, without interlobal plicae; interstaminal glands at the base of the tube (never at the base of the ovary) somewhat scutiform or rounded, swollen or appearing only as green patches on the surface of the tube, the glands never foveate. Stamens 4 or 5, included; filaments linear or variously taper-winged, rarely ciliate at the base; anthers 2-celled, oblong, rarely somewhat triangular, versatile, introrse in the bud but becoming extrorse following dehiscence. Ovary sessile or stipitate; carpels 2, 1-celled, the placentae parietal; stigmas 2, sessile or with a distinct style, oblong to flabelliform or reniform, lobed or entire, revolute or plane. Fruit a cylindrical or ovoid capsule, septicidally dehiscent from the apex. Seeds globose or slightly flattened, angular or caudate, reticulate, papillose or smooth, brown or light tan.

#### KEY TO THE SUBGENERA

- a. Flowers 4-merous; calyx tubular, the lobes with thin hyaline margins, the sinuses with a small inner membrane extending across the base and bearing minute blunt processes; anthers distinctly longer than broad, attached in the upper third; ovules borne over the entire surface of the ovary; seeds oblong, oval, or angular, papillose or caudate.....Subgenus I. *EUBLEPHIS*
- aa. Flowers 4- or 5-merous; calyx tubular, rarely spathiform, the lobes with a green margin, the sinuses without an inner membrane; anthers slightly longer than broad, filaments attached at about the middle; ovules borne in two rows along the margin of each suture, rarely with a third row along the carpel wall between the sutures; seeds globose or slightly flattened, smooth, ecaudate.
- b. Pedicels conspicuously shorter than the subtending internode; corolla orifice naked, or bearing scattered vascular minutely papillose fimbriae, or the fimbriae united to form a single scale extending across the base of each corolla lobe.....Subgenus II. *GENTIANELLA*
- bb. Pedicels conspicuously longer than the subtending internode; corolla orifice bearing two fimbriate scales at the base of each corolla lobe, the fimbriae shortly digitate, evascular, smooth.....Subgenus III. *COMASTOMA*

## SUBGENUS I. EUBLEPHIS (Raf.) J. M. Gillett, comb. nov.

- Gentiana* L. subgenus *Eublephhis* Raf. Med. Fl. 1:208. 1828. (T.: *G. crinita* Froel.)  
*Gentianella* Borckh. in Roem. Archiv f. Bot. 1:29. 1796, non Moench. (T.: *G. ciliata* (L.) Borckh.)  
*Gentiana* L. \*\*\*\* *Crossopetalae* Froel. Gent. Diss. 109. 1796, sine ordine.  
*Denckea* Raf. in Med. Repos. II, 5:352. 1808, nom. nud.  
*Crossopetalum* Roth, Enum. Pl. Phaen. Germ. 1:516. 1827. (T.: *C. gentianoides* Roth = *Gentiana ciliata* L.)  
*Gentiana* L. *Urananthe* Gaud. Fl. Helv. 2:270, 1828, sine ordine.  
*Gentiana* L. sect. *Crossopetalum* Froel. ex Griseb. in Hook. Fl. Bor. Amer. 2:64. 1838.  
*Gentianopsis* Ma, in Acta Phytotax. 1:7. 1951. (T.: *G. barbata* (Froel.) Ma)

Flowers usually large and showy, 4-merous, long-pedicellate. Calyx usually 4-angulate, the lobes with thin hyaline margins, the two inner triangular to ovate, the two outer linear to lanceolate, acute, and usually conduplicate and the margins united at the tips, each sinus with a thin inner membrane bearing few to many blunt processes. Corolla tube without faucal fimbriae, the lobes with reticulate venation connecting the main veins. Stamens inserted near the middle of the tube. Ovary with the parietal placenta extending over most of the inner surface. Seeds ellipsoid to angular, minutely or strongly papillose, or caudate, light brown.

Tetraploids or hexaploids on base numbers of 11 and 13.

Type species: *Gentianella crinita* (Froel.) G. Don.

## KEY TO THE SPECIES

- a. Plants in general branched, occasionally simple (but usually occurring among populations of branched plants), with a definite rosette of basal leaves or a tendency to form a rosette by shortening of the lower internodes; flowers solitary or in axillary or terminal cymes; seeds ecaudate, the surface papillose.
- b. Terminal flowers borne on slender pedicels extending beyond the upper pair of leaves; corolla tube glabrous below the insertion of the stamens; annuals or biennials with tap-roots.
- c. Base of the calyx and the calyx keels smooth or wrinkled, the keels glossy purple; upper leaves usually obtuse.....1. *G. detonsa*
- cc. Base of the calyx near the junction with the pedicel and usually at least one pair of calyx keels covered by whitish or hyaline papillae (under magnification) occasionally present also on the margins of the lobes, the keels green or purple; upper leaves acute.  
.....2. *G. crinita*
- bb. Flowers sessile or shortly pedicellate, the uppermost pair of bract-like leaves immediately below the flower and subtending it; corolla tube bearing rows of long cilia below the insertion of the stamens; perennials from slender rhizomes.....3. *G. barbellata*
- aa. Plants simple, never branched, without a basal rosette of leaves; the single flower borne terminally on an elongate naked pedicel; seeds caudate, the surface reticulate.....4. *G. simplex*

While *G. simplex* and *G. barbellata* are both morphologically and geographically very sharp, clear-cut populations, the *G. detonsa-crinita* complex is much less convincing. The complex may be considered either as one large species or divided into two rather weak species. The presence or absence of papillae on the calyx keels is a constant character differentiating these species. The obtuse or rounded medium leaf tips of the *detonsa* group versus the acute tips of the *crinita* group is a strong supporting character. Other characters either vary considerably or are influenced both by plant age or by the presence of the small form of the plant found so commonly among the larger members of a population.



I have chosen to recognize *G. detonsa* and *G. crinita* as two separate species for the following reasons: 1. *Gentianella crinita* ssp. *crinita* has an Appalachian distribution probably indicating an older history than that of *G. detonsa*. 2. The disjunction between the non-papillose northern *G. detonsa* ssp. *raupii* and the central ssp. *elegans* can be more readily explained. 3. The presence of the narrow-leaved papillose-keeled ssp. *macounii* between these two disjunct populations can best be explained by migration. 4. Present-day scant cytological evidence in the group indicates the presence of at least two chromosome series, the *detonsa* series with a base number of 11 and the *crinita* series with a base number of 13. 5. The occasional presence of sterile and depauperate forms in Manitoba may be due to occasional crosses between members of these two chromosome series.

1. GENTIANELLA DETONSA (Rottb.) G. Don, Gen. Syst. 4:179. 1838.

*Gentiana detonsa* Rottb. Kiob. Selsk. Skr. (Acta Hafn.) 10:435. 1770. (T.: *Collector unknown*, herb. Rottböll, C!)

Annuals or biennials, 0.5–9.0 dm. tall, branched from the base or above, or simple, the basal branches curved or straight, shorter than (or nearly equal to) the main stem. Basal leaves elliptic, obovate-elliptic to spatulate, the apex rounded, obtuse, or acute, attenuate below to about the width of the stem, 0.5–3.5 (–6.0) cm. long, 0.1–1.5 cm. wide, forming a dense rosette, or frequently reduced to one pair; median leaves linear or linear-lanceolate to elliptic or spatulate, usually rounded, the base attenuate to about the width of the stem or slightly broader, frequently subamplexicaul or clasping, 1.5–6.5 cm. long, 0.1–0.7 cm. wide. Flowers solitary and terminal, long-pedicellate, the terminal pedicels 1–30 cm. long, those of the basal or lateral branches when present shorter, occasionally equal. Calyx narrowly to broadly funnelform, the tube 9–14 mm. long, 5–7 mm. wide below the lobes, the inner lobes ovate-triangular, acute, about 10 mm. long, the outer lobes longer, lanceolate and conduplicate, frequently carinate at the tip, acute, up to 14 mm. long or equal to the inner lobes; keels 1 mm. or less wide, scarcely prominent, smooth and reticulate, generally purple-tinged; sinuses acute, covered on the inside by a small straight to sulcate membrane extending to the center of the outer lobes and bearing few to many blunt processes up to 0.5 mm. long. Corolla pale to dark blue, narrowly funnelform, 2–4 (–5) cm. long, 4–10 (–15) mm. wide at the orifice, the lobes oblong or somewhat expanded above, 9–15 mm. long, 5–7 (–15) mm. wide, the tips erose to denticulate, the margins with few to several cilia 0.5–1.5 mm. long in the lower half. Stamens included, the filaments inserted near the middle of the corolla tube, the marginal wings 1.5 mm. wide at the base, tapering gradually above; anthers 2.5 mm. long, 1.0 mm. wide, attached above the middle; interstaminal glands oblong, crescent shaped to rounded, swollen below and tapering to the tube above. Pistil short-stipitate, the gynophore 2–4 mm. long, obscurely attenuate; ovary fusiform, about 12 mm. long, 2.0 mm. wide; stigmas sessile or short-stipitate, flabelliform, reniform, or oblong, 1.75 mm. wide. Capsule as long as the corolla tube or slightly longer, dehiscing in the upper

third, the tips of the valves recurving. Seeds ovoid to oblong, slightly flattened, the surface reticulate and with slender or rounded, inflated or somewhat collapsed hyaline papillae irregularly dispersed or concentrated at the angles and ends.

Circumboreal, extending from North America to Europe through Greenland and Iceland, and to Asia through Siberia; in North America from both the east and the west coasts of Greenland as far north as Disko and Cape Oswald, on the mainland westward to Coppermine and Kotzebue, southward on the east to Quebec and Newfoundland and on the west through Alaska and the Yukon through the Rocky Mountains and the Sierra Nevada to the Sierra Madre of Mexico; resolving into several subspecies and numerous minor local variants.

In a variety of habitats: tidal estuaries, river banks, mountain meadows, saline meadows, about hot springs and sloughs, in open or sparsely wooded plains, but in general preferring lime soils or shallow soil over limestone; flowering and fruiting times various depending upon latitude but generally from late June until November; at altitudes from sea-level to 2500 meters.

#### KEY TO THE SUBSPECIES

- a. Margins of the corolla lobes ciliate at least in the lower half, the tips erose to dentate; pedicels 2–15 cm. long; gynophore short, never as long as the capsule; interstaminal glands not swollen.
- b. Seeds oblong with smoothly rounded ends, the elongate inflated or collapsed and scale-like whitened papillae restricted to the ends, occasionally absent; calyx tube attenuate to the pedicel, not abruptly constricted; corolla slender, 4–9 mm. wide at the frequently constricted or scarcely expanded orifice, the tube narrowly obconic. Arctic coast and west of the Mackenzie Mountains.
- c. Plants 0.5–1.8 dm. tall, simple or the branches arising from the base; basal rosette poorly developed or reduced to a single pair of leaves. Circumboreal above the northern limit of trees, Kotzebue to Coppermine and the coast of Greenland.....1a. *G. detonsa* ssp. *detonsa*
- cc. Plants 2–6 dm. tall, simple or the branches arising from the axils of cauline leaves, rarely from the base; basal rosette well developed, the leaves dense, rarely reduced particularly in smaller specimens. Yukon and Alaska, chiefly along the Yukon River and its tributaries.....1b. *G. detonsa* ssp. *yukonensis*
- bb. Seeds irregularly angled, the rounded, inflated, light-brown papillae distributed over most of the surface; calyx tube abruptly constricted to the pedicel; corolla 8–15 mm. wide at the distinctly expanded orifice, the tube rather broadly obconic or poculiform.
- d. Flowers 1–4 cm. long, rarely longer, 0.5–1.2 cm. wide at the orifice, the keels of the calyx not prominent; cauline leaves elliptic to spatulate.
- e. Plants usually short, 0.5–1.2 (–2.0) dm. high, profusely branched from the densely spatulate-leaved base, the green or purpled branches curved-ascending; corolla lobes somewhat short and truncate, about  $\frac{1}{3}$  to  $\frac{1}{2}$  the length of the tube. East coast of James Bay, Anticosti and Newfoundland.....1c. *G. detonsa* ssp. *nesophila*
- ee. Plants generally tall, 3–6 dm. high, branched above, occasionally simple in small plants, the branches and stem frequently sinuous and strongly purpled; corolla lobes elongate and rounded, about equal in length to the corolla tube. A highly variable complex extending from the Mackenzie Valley east to Hudson Bay.....1d. *G. detonsa* ssp. *raupii*
- dd. Flowers up to 7 cm. long and 1.6 cm. wide at the orifice, the keels of the calyx prominent, particularly at the base of the tube; cauline leaves lanceolate to elliptic.
- f. Terminal pedicels of mature plants 4–12 (–16) cm. long; flowers 3–5 (–7) cm. long; plants generally branched from the base. Central Rocky Mountain states.....1e. *G. detonsa* ssp. *elegans*
- ff. Terminal pedicels 9–30 cm. long; flowers 4.5–8.0 cm. long; plants generally branched above the base. Southern Arizona; in the Sierra Madres south to Zacatecas.....1f. *G. detonsa* ssp. *superba*

- aa. Margins of the corolla lobes entire, devoid of any fimbriae or teeth, the tips entire to erose; pedicels 2–3.5 cm. long.
- g. Plants 4–9 dm. tall, branched in the upper part, rarely simple; gynophore short, about 5 mm. long; calyx keels rarely papillose; interstaminal glands frequently free at the base and pendent. Southern Sinaloa and Zacatecas to Michoacán...1g. *G. detonsa* ssp. *lanceolata*
- gg. Plants 0.3–4.5 dm. tall, branched from the base or simple; gynophore frequently almost as long as the capsule, 8–11 mm. long; calyx keels always smooth; interstaminal glands swollen below and fused to the corolla tube. California to western Nevada and Idaho.  
.....1h. *G. detonsa* ssp. *holopetala*

1a. GENTIANELLA DETONSA (Rottb.) G. Don, ssp. DETONSA

- Gentiana ciliata* Gunn. Fl. Norv. 2:88. t. 2. f. 3–5. 1772, ex ic.
- Gentiana serrata* Gunn. loc. cit. 2:101. 1772, ex char.
- Gentiana ciliata* Pall. Fl. Ross. 1<sup>2</sup>:101. t. 92. f. 2a. 1788, ex ic.
- Gentianella serrata* (Gunn.) Borckh. in Roem. Archiv f. Bot. 1:29. 1796.
- Gentiana barbata* Froel. Gent. Diss. 114. 1796, ex char.
- Gentiana serrata* Gunn.  $\beta$  *detonsa* (Rottb.) Wahl. Fl. Lapp. 71. 1812.
- Gentiana barbata* Froel.  $\beta$  *simplex* Bunge, in Nouv. Mem. Soc. Nat. Mosc. 1:224. t. 9. f. 1. 1829, ex ic.
- Gentiana brachypetala* Bunge, loc. cit. 225. t. 9. f. 3. 1829, ex ic.
- Gentiana barbata* Froel.  $\gamma$  *Richardsoniana* Macnab, in Edinb. New Phil. Jour. 19:62. 1835. (T.: *Richardson s.n.*, MO, photo!)
- Anthopogon detonsa* (Rottb.) Raf. Fl. Tellur. 3:25. 1837.
- Anthopogon barbata* (Froel.) Raf. loc. cit. 25. 1837.
- Gentiana detonsa* Fries  $\beta$  *barbata* (Froel.) Griseb. in Hook. Fl. Bor.-Amer. 2:64. 1838.
- Gentiana detonsa* Fries  $\gamma$  *simplex* (Bunge) Griseb. loc. cit. 1838.
- Gentiana detonsa* Rottb. var. *groenlandicum* Vict. in Contr. Lab. Bot. Univ. Montréal 20: 18. 1932. (T.: *Porsild & Porsild s.n.*!)
- Gentiana richardsonii* Porsild, in Nat. Mus. Can. Bull. No. 121:274–275. 1951. (T.: *Porsild 2653!*)
- Gentianopsis barbata* (Froel.) Ma, in Acta Phytotax. 1:8. 1951. (Synonyms referring to other Eurasian types are not included).

Subspecies *detonsa* has a circumboreal distribution but appears to occupy rather localized areas within its range. It occurs in Finland, Norway and Iceland, on both east and west coasts of Greenland, in America and Asia. Between Greenland and Coppermine, District of Mackenzie, the disjunction in distribution is constantly being reduced by additional collections. Westward, subspecies *detonsa* occurs at Atkinson Point at the mouth of the Mackenzie, at Kotzebue Sound, and after a further gap, in Mongolia and Siberia, being notably absent from Kamchatka.

Found in moist meadows, along sandy sea beaches; flowering from mid-July to early August; fruiting in August.

I have included *G. barbata* within the synonymy of this subspecies in order to emphasize that the name *barbata* should not be applied to our North American material. *G. barbata*, if considered to be distinct at a later date, applies to the taller Eurasian material and appears to be transitional to ssp. *detonsa*. In this view I follow in part Grisebach, because I have had little European material at my disposal. However, our North American material in my opinion is not identical with the taller European material nor with the various species from Asia illustrated by Yu-chuan Ma in his recent revision.

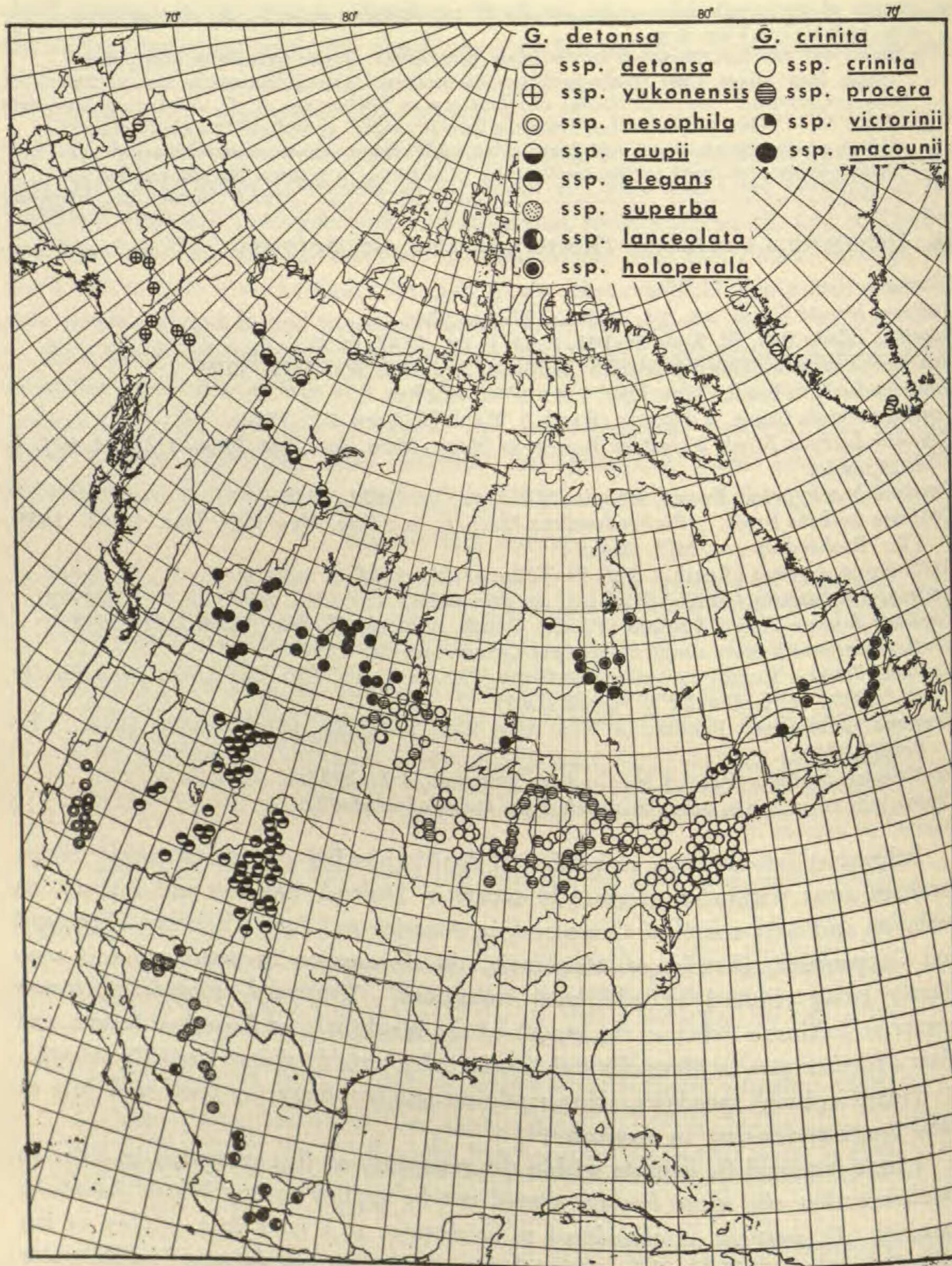


Fig. 1A. Distribution of the subspecies of *Gentianella detonsa* and of *G. crinita*.

NOTE: Through an error in drawing, the symbols for *G. detonsa* ssp. *nesophila* and ssp. *holopetala* have been interchanged.

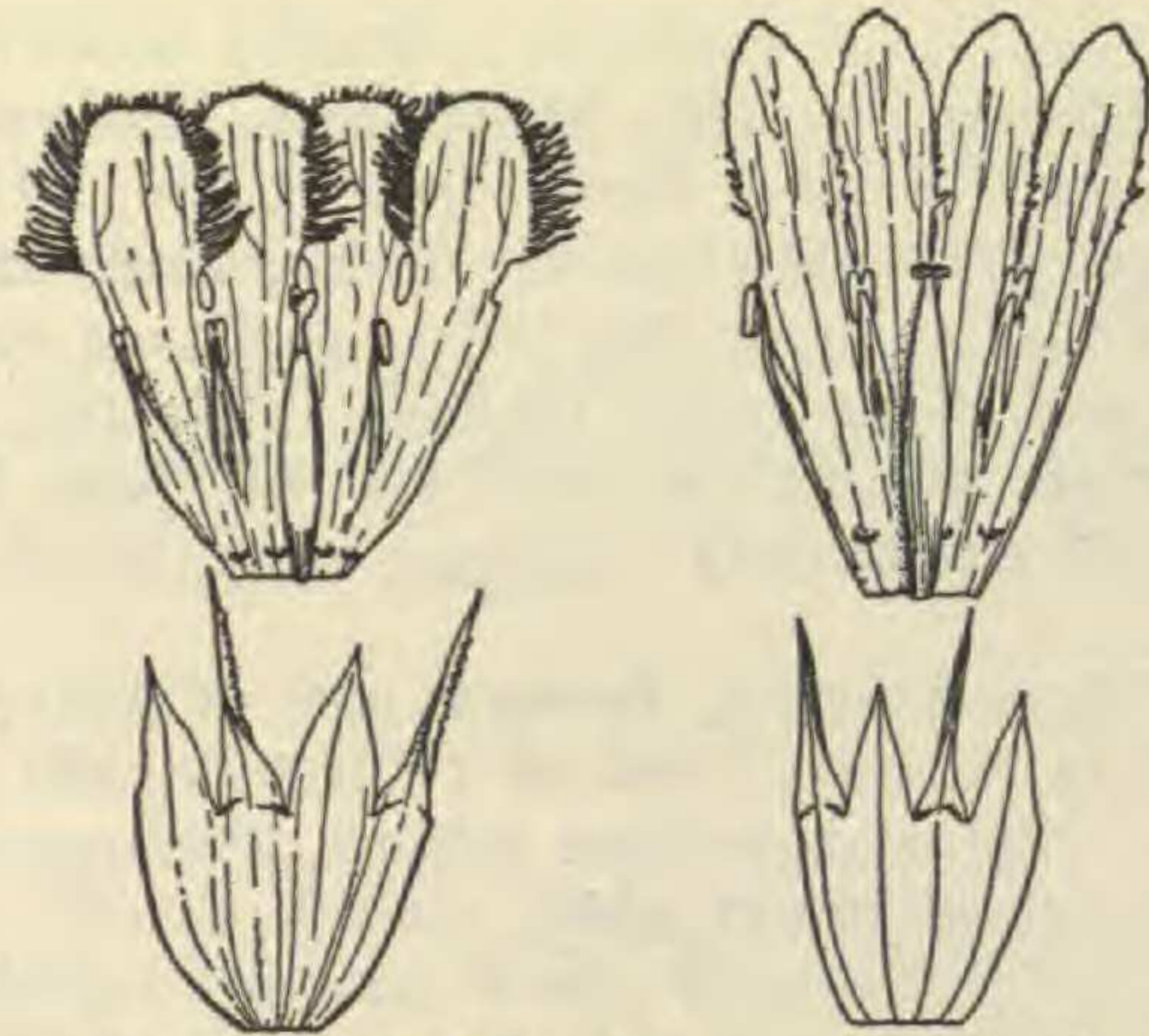


Fig. 1B. Calyx and corolla of *Gentianella detonsa* ssp. *detonsa* (right, approx. nat. size) and of *G. crinita* ssp. *crinita* (left,  $\times \frac{1}{2}$ ).

UNITED STATES:

ALASKA: Keewalik Spit, *Miller 25c* (US); Kotzebue, *Anderson 4683b* (S), *4766* (S), *Lepage 25406* (DAO), *Scamman 4063* (GH), *4663* (CAN).

GREENLAND: Igdungujak, *Hott s. n.* (C); Ekaluit i Igalikofjord, *Lindemann s. n.* (C); Itivdleq-Fjord, Qingua, *Porsild s. n.* (C, CAN, MO, US); Igaliko (Gardar), *Porsild & Porsild s. n.* (C, CAN, GH, JBM, US), *Rosenvinge s. n.* (C, CAN), *Vahl s. n.* (C); Julianehaab, *Rosenvinge s. n.* (C), *Vahl s. n.* (C), *Porsild 8085* (CAN).

CANADA:

MACKENZIE: Coppermine, *Findlay 241* (DAO); Atkinson Point,  $70^{\circ}$  N,  $131^{\circ}$  20' W, *Porsild & Porsild 2653* (CAN).

1b. GENTIANELLA DETONSA (Rottb.) G. Don, ssp. *yukonensis* J. M. Gillett, subsp. nov.

Herbae annuae. Caules erecti, 2–6 dm. alti, simplices sive ramosi, ramis ex axillis foliorum caulinarium interdum radicalium emergentibus. Folia radicalia pluralia in rosulam congesta elliptica vel spathulata apice obtusa, 6–25 mm. longa, 5–10 mm. lata; folia media linearia vel lineari-lanceolata, 20–60 mm. longa, 1–6 mm. lata. Flores et semina subspeciei typica similes.

Although variation in subspecies *detonsa* is rather high and the distribution is circumboreal, there appears to be considerable justification in erecting this new subspecies based chiefly on size difference and mode of branching. A prominent morphological feature is the dense rosette of basal leaves. Floral and fruit morphology is essentially similar to the typical subspecies but the flowers are slightly larger. Habitat data appearing only on modern collections show that it is found in sandy and gravelly places. *Cody & Webster 5587* has been selected as the type because the material is of good quality and because several duplicate sheets are available for distribution.

The range of subspecies *detonsa* corresponds rather closely to that region north of the Nordenskiöld line which in turn roughly corresponds to the northern limit of trees in North America. Subspecies *yukonensis* occurs south of this line and apparently is restricted to the valley of the Yukon River and its tributaries.

## UNITED STATES:

ALASKA: Tanacross, *Anderson s. n.* (S); Mackintosh, *Anderson & Brown 10065* (S); between Summit and McCarty, *Porsild & Porsild 440* (CAN, GH, US); near Delta Junction, *Cody & Webster 5599, 5717* (DAO); Big Delta, *Cody & Webster 6154* (DAO), *Lepage 25325* (CAN); Buffalo Center nr. Big Delta, *Anderson 8939* (CAN); Fort Yukon, *Houle s. n.* (CAN); scattered along sandy roadside, Mile 265, Richardson Highway, 4 miles south of Delta Junction, 60° 00' N, 145° 45' W, June 28, 1951, *W. J. Cody & T. J. M. Webster 5587* (DAO, HOLOTYPE).

## CANADA:

YUKON: Pelly River, Mayo District, *Bostock 226* (CAN); Ranch Valley, *Gorman 1081* (CAN, NY, US); Snag Airport, *Noel 38* (UBC), *14184* (CAN); Lake Kluane to Don Jek River, *Müller s. n.* (PH); above Fort Selkirk, *Tarleton 115a* (US), *115b* (NY); Cormacks, Yukon River, *Eastwood 567* (CAN).

1c. GENTIANELLA DETONSA (Rottb.) G. Don, ssp. *nesophila* (Th. Holm)  
J. M. Gillett, comb. & stat. nov.

*Gentiana nesophila* Th. Holm, in *Ottawa Nat.* 15:11. 1901. (T.: *Macoun s. n.*!)

Northwestern Newfoundland, the Mingan Islands and Anticosti, and on the east coast of James Bay, on sandy or gravelly calcareous soil, at elevations from sea level to about 20 meters; flowering from late July until early September, fruiting from August until October.

## CANADA:

KEEWATIN: Boat Opening, Manitounuk Island, *Dutilly & Lepage 12944* (DAO), *13021* (CAN); South Twin Islands, *Johansen 273* (CAN).

NEWFOUNDLAND: Cape St. George, *Mackenzie & Griscom 11121* (GH); Cape Norman, *Wiegand & Long 28927* (GH); Cook Point, *Fernald, Gilbert & Hotchkiss 28928* (GH); Brig Bay, *Fernald, Long & Dunbar 26969* (GH); Cow Head north of St. Paul's Bay, *Fernald & Wiegand 3898* (GH); Port au Port ("The Gravels"), *Fernald & Wiegand 3900* (CAN, GH, US); Old Ferolle, *Huntsman s. n.* (GH); Flower's Cove, *Fernald, Long & Dunbar 26970* (GH); Straits of Belle Isle, Mistaken Cove, *Fernald, Long & Dunbar 26966* (GH); Raleigh, *Jeffers 141* (GH); Old Port au Choix, St. Barbe, *Tuomikoski 355* (CAN); St. John Bay, Bard Harbour, *Fernald & Long 28925* (GH); Savage's Island, *Fernald, Long & Fogg 1959* (GH); St. Barbe, *Fernald, Long & Dunbar 26967* (GH, US); Bonne Bay, *Fernald, Long & Fogg 1961* (GH); Ingornachoix Bay, *Fernald & Wiegand 3899* (GH).

ONTARIO: Attawapiskat, *Dutilly & Lepage 15797* (CAN).

QUEBEC: Anticosti Island, nr. Salt Lake, *Macoun s. n.* (CAN); mouth of Jupiter River, *Wyatt, Shaler & Verrill, s. n.* (GH), *Rousseau 52411* (JBM), *Victorin & Rolland 25137* (CAN), *25197* (GH, US); Sand-top, *Victorin, Rolland & Louis-Marie 21069* (CAN, GH, MO, US); Mingan Islands, *Victorin & Rolland 21068* (GH, MO); Ile Sainte-Genevieve, *Victorin & Rolland 21066* (GH); Pointe de Betchouane, *Victorin & Rolland 21067* (CAN, GH, MO, US); James Bay, Baie aux Oies, *Lepage 12927* (CAN, DAO, JBM); Fort George, *Low s. n.* (CAN); Vieux Comptoir, *Dutilly & Lepage 13389* (CAN), *32057* (JBM); Kegashka Bay, *Lewis s. n.* (CAN).

The population of ssp. *nesophila* is relatively distinct but there are occasionally specimens from Newfoundland that resemble the typical subspecies rather closely. James Bay material frequently approaches ssp. *raupii* (for example, *Lepage 12877*, CAN).

- 1d. *GENTIANELLA DETONSA* (Rottb.) G. Don, ssp. *raupii* (Porsild) J. M. Gillett, comb. & stat. nov.

*Gentiana raupii* Porsild, in *Sargentia* 4:60. 1943. (T.: *Porsild 6571!*)

Sandy river shores, clay banks and salt plains along the Mackenzie River basin at low elevations, with scattered stations along Hudson Bay; flowering from late June to early August; fruiting in August.

CANADA:

ONTARIO: Raft River, James Bay [?], *Spreadborough s. n.* (CAN); Weenusk, *Dutilly & Lepage 16925* (DAO); Swan River, *Lepage 31666* (DAO).

MACKENZIE DISTRICT: Wood Buffalo Park, Moose Lake, *Raup 3026* (CAN); Fort Norman, *Kindle s. n.* (CAN); Norman Wells, *Wynne-Edwards 8564* (CAN); Ramparts, Mackenzie River, *Porsild & Porsild 3403* (CAN); Great Bear Lake, McVicar Arm, *Wynne-Edwards 8617* (CAN); Heart Lake, *Raup 3028* (CAN); Great Slave Lake, *Howe 1026* (CAN); Sulphur Bay, *Howe s. n.* (CAN); Brabant Island, *Lewis 1074* (DAO); Mackenzie River betw. Wrigley and Blackwater River, *Porsild 6571* (CAN, photo DAO), *Crickmay s. n.* (CAN); Hay Camp District, Slave River, *Raup 3027* (CAN); Fort Wrigley, *Lindsey 296* (CAN); Mackenzie delta, east branch, *McEwan 47* (CAN); Fort Simpson, *Nowosad 4* (DAO); Fort Smith, *Cody & Loan 3783, 4169* (DAO); Mackenzie River, *Hutton s. n.* (DAO), *Jones s. n.* (CAN).

This subspecies must for the present remain a *pot-pourri* for that heterogenous assemblage of material occupying the Mackenzie Valley and extending to Hudson Bay in the east. The southern boundary of the subspecies is ill defined because the northern prairie provinces and southern districts of Mackenzie and Keewatin are still poorly collected. In the Hudson Bay and James Bay regions some specimens approach ssp. *nesophila*.

As the *detonsa* complex invaded the regions formerly occupied by the ice the movement was apparently accompanied by a segregation of numerous minor local variants. Variation was also produced by local environmental factors and resulted in a bewildering array of forms any of which may crop up with little regard for geographical continuity.

- 1e. *GENTIANELLA DETONSA* (Rottb.) G. Don, ssp. *elegans* (A. Nels.) J. M. Gillett, comb. & stat. nov.

*Gentiana thermalis* O. Ktze. *Rev. Gen.* 2:427. 1891, ex char. (T.: *Kuntze s. n.*)

*Gentiana elegans* A. Nels. in *Bull. Torr. Bot. Club* 25:276. 1898. (T.: *A. Nelson 1539!*)

*Gentiana elegans* A. Nels. var. *unicaulis* A. Nels. loc. cit. 277. 1898. (T.: *Nelson 4173!*)

*Gentiana elegans* A. Nels. var. *brevicalycina* Wettst. ex Th. Holm, in *Ottawa Nat.* 15:182. 1901, ex char.

*Anthopogon elegans* (A. Nels.) Rydb. in *Bull. Torr. Bot. Club* 33:148. 1906.

*Anthopogon thermalis* (O. Ktze.) Rydb. in *Fl. Rocky Mts.* 659. 1917.

I have followed the general practice of employing the oldest specific epithet for my subspecies in accordance with Recommendation 71A, Part 2 of the Rules (1950 ed. Stockholm). In some cases, however, where doubt exists concerning the location or identity of the type of the earliest specific name, I have chosen the next epithet for which a widely distributed or well-preserved type exists. The epithet *elegans* has been selected here, rather than *thermalis*, because it is more

widely known and because Nelson's specimen is of fine quality and is distributed among at least three herbaria and probably more. Kuntze's specimen has not been found. Rydberg, in making the combination *Anthopogon thermalis*, remarked "*G. thermalis* Kuntze, based on depauperate specimens."

Common throughout the Rockies from southern Montana to Wyoming, Utah and Idaho, west to eastern Nevada, south to New Mexico; in mountain meadows and along streams and roadsides; frequent about hot springs; flowering throughout July and August; fruiting in late August and September.

UNITED STATES:

COLORADO: Archuleta Co.: Chromo, Wootton 2910 (US). Boulder Co.: Ward, Clokey 2741 (US). Chaffee Co.: Buena Vista, Maguire & Piranian 12856 (GH, MO). Clear Creek Co.: Wet Mountain Valley, Horner s. n. (GH). Conejos Co.: Cumbres Pass, Babcock 9666 (GH). Custer Co.: Sangre de Cristo Range, Ewan 15390 (GH). Eagle Co.: Leadville Forest, Eggleston 11780 (US). Garfield Co.: Trapper's Lake, Hermann 5472 (GH, MO, US). Grand Co.: Middle Park, Grand Lake, Engelmann s. n. (MO); Shapler Park, Clokey & Clokey 4238 (MO, US, WS). Grant Co.: Rabbit Ears Pass, Baker 7 (US). Gunnison Co.: Kebler Pass, Baker 785 (GH, MO). Jackson Co.: Mt. Richtophen, Baker 6 (US). Lake Co.: Twin Lakes, Wolf 789 (US). La Plata Co.: Rockwood, Evermann s. n. (US). Larimer Co.: Cameron Pass, Baker s. n. (MO); Estes Park, Allen 113 (MO). Mineral Co.: Pagosa Peak, Baker 522 (GH, MO, US). Park Co.: South Park, Jefferson, Letterman s. n. (MO). Routt Co.: Columbine, Tweedy 4098 (US). San Juan Co.: Silverton, Popenoe s. n. (MO, PH). San Miguel Co.: Trout Lake, Payson & Payson 4116 (GH, MO). Summit Co.: Breckenridge, Brandegee s. n. (MO, NY).

IDAHO: Bannock Co.: Blackfoot River, Eggleston 10002 (US). Bingham Co.: 10 mi. nw. Gray's Lake, Gillett, Senn & Frankton 6039 (DAO). Fremont Co.: Henry's Fork, Snake River, Coulter s. n. (US); Henry's Lake, Rydberg & Bessey 4695 (GH, US).

MONTANA: Carbon Co.: Rock Creek, Elliott 76 (DAO, GH). Gallatin Co.: Gallatin basin, Blankinship 351 (MO, US); 8 mi. w. Eldridge, Hitchcock & Mublick 15132 (MO, WS). Madison Co.: Beaver Creek, Hitchcock & Mublick 15120 (MO, WS); Madison Forest, Schwan s. n. (ID). Park Co.: 2 mi. s.e. Cooke City, Hitchcock & Mublick 13617 (GH, MO, US, WS). Stillwater Co.: Absaroka Nat. Forest, Hitchcock & Mublick 13406 (MO, WS).

NEVADA: Elko Co.: Ruby Valley, Heller 9531 (GH, MO, NY, PH, US). Eureka Co.: Brandegee s. n. (MO).

NEW MEXICO: Colfax Co.: Ute Park, Standley 14469 (GH, US). Mora Co.: Santa Fe Forest, Eggleston 19031 (NY, US). Santa Fe Co.: Santa Fe, Alcott s. n. (MO). Taos Co.: La Junta Canyon, Marcelline 2150 (F, WS). Sandoval Co.: Jemez Mts., Goodwin s. n. (GH).

UTAH: Custer Co.: Wet Mountain Valley, Bacigalupi 983 (GH). Grand Co.: La Sal Mts., Payson & Payson 4075 (GH, MO). Iron Co.: Cedar Canyon, 15 mi. e. Cedar City, Hitchcock, Rethke, & Van Raadshooven 4635 (US, WS). Emery Co.: 10 mi. w. Castle Dale, Maguire & Richards 15931 (GH, MO). Sanpete Co.: e. of Mount Pleasant, Tidestrom 1887 (US). Sevier Co.: Fish Lake, Jones 5777 (US). Summit Co.: La Motte Peak, Jones s. n. (MO, US), Payson & Payson 5108 (GH, MO, US); Wasatch Mountains, Clos 130 (US). Wayne Co.: Rabbit Valley, Ward 607 (MO, US).

WYOMING: Albany Co.: Medicine Bow Mts., Nelson 1539 (GH, MO, RM); Lincoln Gulch, Nelson 8007 (GH, MO, US); Centennial, Nelson 8709 (GH, MO, US); Telephone Mines, Nelson 7888 (GH, MO, US). Carbon Co.: Medicine Bow Mts., Silver Lake, Ownbey 325a (WS). Lincoln Co.: Grey's River, Porter 5175 (DAO). Park Co.: Shoshone Nat. Forest, Beartooth Lake, Williams & Williams 3728 (GH, MO). Sublette Co.: Wind River Mts., Forwood s. n. (US); Surveyor Park, Fremont Lake, Payson & Payson 2827 (GH, MO). Teton Co.: Jackson's Lake, Merrill & Wilcox 1082 (GH, US). Yellowstone National Park: Lower Geyser Basin, Thompson 14159 (GH, MO, US, WS); Upper Geyser Basin, Mearns 473 (US); Yellowstone Lake, Nelson & Nelson 6764 (GH, MO, US).



- 1f. *GENTIANELLA DETONSA* (Rottb.) G. Don, ssp. *superba* (Greene) J. M. Gillett, comb. & stat. nov.

*Gentiana macrocalix* Lex. in La Llave & Lex. Nov. Veg. Descr. 1:19. 1824, ex char.  
*Gentianella macrantha* D. Don, ex G. Don, Gen. Syst. 4:179. 1838, ex char.  
*Gentiana ciliata* Moc. & Sessé, ex G. Don. loc. cit. 119. 1838, nom nud. in syn.  
*Gentiana macrantha* (D. Don, ex G. Don) Griseb. in DC. Prod. 9:102. 1845.  
*Gentiana serrata* Gunn. var. *grandis* A. Gray, Syn. Fl. N. Amer. 2:116. 1886. (T.: Wright 1658!)  
*Gentiana superba* Greene, Pittonia 1:155. 1888. (T.: Forrer 44!)  
*Gentiana grandis* (A. Gray) Th. Holm, in Ottawa Nat. 15:110. 1901.

As explained under ssp. *elegans*, I have tried to select as subspecific names the earliest ones available, or those most widely known (although not obliged to do so). I believe this course more reasonable than to propose entirely new names. In ssp. *superba* the earliest name was not selected because of difficulty in the identity or location of types.

The type of *Gentiana macrocalix* Lex. is given as "Habitat prope Vallisoletum et Irapaeum. Floret Novembri—Lex." The type has not been seen. "Irapaeum" is probably Uruapan (del Progreso) in Michoacán. The description is not sufficiently clear to enable positive identity with the north Mexican population. The actual type locality may be within the range of ssp. *lanceolata*.

The next available name, *macrantha*, also exhibits difficulties, for the type is a Sessé & Mociño collection. The type has not been seen but a photograph at Chicago and a Sessé & Mociño sheet at the Gray Herbarium yield no locality data. According to Hemsley (Jour. Bot. n. s. 8:275. 1879), Drs. Parry and Palmer later collected in the State of San Luis Potosí in essentially the same region as did Mociño & Sessé. The exact locality is still uncertain but still may be somewhat outside the range of this subspecies.

The name *grandis* is avoided because of the possibility of confusion with *Gentiana grandis* H. Sm. (Anz. Akad. Wiss. Wien, math.-nat. Cl. 63:100. 1926).

Greene's name for which the type Forrer 44 (UC) plus two isotypes (F, GH) have been seen and for which the locality is known is thus employed. *G. macrocalix* and *G. macrantha* are placed in synonymy provisionally.

Arizona in the Huachuca and Santa Rita mountains, in the Sierra Madre of Chihuahua south to Durango and Zacatecas at altitudes of 2000–2600 meters; in moist areas and roadsides, steep open slopes, and in open pine forest; flowering from September until late November.

UNITED STATES:

ARIZONA: Cochise Co.: Huachuca Mts., Lemmon 2823 (PH, US), 2883 (GH); Fort Huachuca, Wilcox 489 (US). Santa Cruz Co.: Santa Rita Mts., Peebles & Harrison 2955 (US), Wootton s. n. (US).

MEXICO:

CHIHUAHUA: Palmer 361 (GH, NY, US); Santa Brigida, Hewitt 88 (GH); Sierras near Huajochic, Lumboltz s. n. (GH); Sierra Madre, Mound Valley, Jones s. n. (US); near Guachochi, Goldman 173 (GH, US); San Julian, Nelson 4942 (GH, US); Memoriali, Rio Mayo, Gentry 2726 (F, GH, MO, UC); 10 mi. s.e. Colonia Garcia, Townsend & Barber 320 (F, NY); south Chihuahua, Zingg s. n. (F).

DURANGO: Sierra Madre, west of Durango, *Forrer 44* (F, GH, UC); Rosilla, *Collins & Kempton s. n.* (US); El Salto, *Martinez s. n.* (F).

SONORA: *Wright 1658* (GH, MO, NY, PH, US); Batocomori and Santa Cruz, *Thurber 926* (GH, NY).

ZACATECAS: Sierra de Valparaiso, *Goldman 6* (GH, US).

LOCALITY UNKNOWN: *Sessé & Mociño 685, 1371* (F), *s. n.* (GH, photo F).

1g. *GENTIANELLA DETONSA* (Rottb.) G. Don, ssp. *lanceolata* (Benth.) J. M. Gillett, comb. & stat. nov.

*Leianthus lanceolatus* Benth. Pl. Hartw. 24. 1839. (T.: *Hartweg 209!*)

*Gentiana lanceolata* (Benth.) Griseb. in DC. Prod. 9:102. 1845.

Mexico from perhaps southwestern Chihuahua in the Sierra Madre to Michoacán, and in Vera Cruz about Cofre de Perote; altitude unknown; flowering from early September to late November; fruiting during November and December.

MEXICO:

JALISCO: Bolanos, *Hartweg 209* (GH, photo DAO, MO).

GUANAJUATO: *Duges 27* (GH).

MICHOACAN: Patzcuaro, *Pringle 3941* (F, GH, MO, NY, US); Morelia, *Arsène s. n.* (US).

SINALOA: Cueva del Diablo, *Debesa 1562* (US).

ZACATECAS: Sierra de los Morones, Plateado, *Rose 2716* (F, GH, NY, US).

Subspecies *lanceolata* is distinguished chiefly by the entire corolla lobes, relatively slender flowers, and linear leaves. In Zacatecas, where the range overlaps that of ssp. *superba*, the flowers are larger and leaves broader. Since the material at hand is scant and extremely variable, it is difficult to elaborate further on this apparently clinal effect. However, such observations as have been possible indicate a low genetic barrier separating these two subspecies. The north-south trend of variation and the overlapping range seem to justify the recognition of this population merely as a subspecies of *G. detonsa*.

Mention should be made of a specimen collected by E. K. Balls (5438, US!) from Cofre de Perote, Vera Cruz. This specimen has shorter, more linear leaves than the other specimens of ssp. *lanceolata* and the corolla is more narrowly funnel-form and attenuate to the pedicel. One interesting feature is the habitat, which Balls describes as: "bog, among rushes, etc." Since the slight morphological difference may be due only to environmental conditions, and because the range of variability is high in this group, no taxonomic recognition is given here to this collection.

1h. *GENTIANELLA DETONSA* (Rottb.) G. Don, ssp. *holopetala* (A. Gray) J. M. Gillett, comb. & stat. nov.

*Gentiana serrata* Gunn. var. *holopetala* A. Gray, Bot. Calif. 1:481. 1876. (T.: *Bolander 6359!*)

*Gentiana holopetala* (A. Gray) Th. Holm, in Ottawa Nat. 15:110. 1901.

Sierra Nevada Mountains in open wet meadows, hillsides, gravelly places and about springs in the Canadian and Hudsonian life zones, at altitudes of 2600–3300 meters; flowering from early July until about the end of August; fruiting in late August until the middle of September.

## UNITED STATES:

CALIFORNIA: Calaveras Co.: Murphy's, *Lemmon 1137* (GH). Fresno Co.: Silver Pass, *Grant 1516* (MO). Inyo Co.: Cottonwood Lakes, *Alexander & Kellogg 3324* (GH, MO). Madera Co.: Upper San Joaquin, *Congdon s. n.* (MO). Mariposa Co.: Sierra Nevada, *Bolander 6359* (GH, MO, US). Mono Co.: Bloody Cañon, *Chesnut & Drew s. n.* (US); Sonora Pass, *Wiggins 9522* (CAN, GH, WS). Mono-Madera Cos.: Yosemite Nat. Park boundary, *Evans s. n.* (F). Placer Co.: Lake Tahoe region, *Smith s. n.* (F). Plumas Co.: *Austin s. n.* (GH). Sierra Co.: *Lemmon s. n.* (GH, PH). Tulare Co.: Nat. Bridge Meadow, *Culbertson 4260* (GH, F, MO); South Fork, Kern River, *Rothrock 313* (MO, PH, US). Tuolumne Co.: Tuolumne Valley, *Brewer 2847* (MO, US).

NEVADA: Boat Corral, *Coville & Funston 85* (US).

*Gentianella detonsa* ssp. *holopetala* is easily recognized by the long gynophore, entire corolla lobes, and the usually acute cauline leaves. Since these characters are variable, it seems advisable to consider the Californian population at a rank lower than species. Furthermore, occasional specimens superficially are very similar to specimens of subspecies *detonsa* from Alaska. The one Nevada collection seen resembles ssp. *elegans*, so that these subspecies may also intergrade. The Nevada collection lacks adequate data to enable it to be plotted.

An interesting character of ssp. *holopetala* is the almost hyaline wedges in the corolla tube below the sinuses, which in many herbarium specimens appear to be somewhat slack, rather suggesting the plicae between the lobes in *Gentiana*. For this reason many collections have been misidentified as *Gentiana newberryi* Gray. However, the "plicae" of ssp. *holopetala* are vascularized; those of *Gentiana* are not.

In his flora, Jepson<sup>54</sup> cited the type of *holopetala* as *Brewer 2847*. Gray, however, cited Bolander as the collector but gave no collection number. Bolander had a collection number 2847, so that Jepson's error may have been due to a confusion of the names of the collectors. This plant is the dwarf plant mentioned by Gray; the Yosemite plant (*Bolander 6359*) is more typical and was also cited by Gray. To avoid further confusion, I consider this latter specimen, *Bolander 6359*, as the type.

2. GENTIANELLA CRINITA (Froel.) G. Don, Gen. Syst. 4:179. 1838.

*Gentiana crinita* Froel. Gent. Diss. 112. 1796, ex char.

Annuals (biennials or winter annuals?), 1–6 dm. tall, branched from the base or above, or simple. Basal leaves lingulate to spatulate, the apex rounded, obtuse or acute, the base attenuate to the stem, 0.8–1.6 (–3.3) cm. long, 0.1–0.6 (–1.0) cm. wide, soon withering or deciduous; median leaves linear, linear-oblong, lanceolate-ovate to ovate, elliptic in small forms, usually acute, the base attenuate to the width of the stem, or rounded or subcordate and clasping, 1.0–8.0 cm. long, 0.1–2.0 cm. wide. Flowers few to very numerous, or solitary, the terminal pedicels

<sup>54</sup> Jepson, Fl. Calif. 3<sup>1</sup>:88. 1939.

2–22 cm. long, those of the branches usually shorter. Calyx narrowly to broadly funnelform, the tube 8–15 mm. long, 5–15 mm. wide below the sinus, the inner lobes ovate-triangular, subulate to acute, the outer lobes longer, lanceolate and conduplicate, the margins frequently carinate near the tip, acute, longer than or equal to the inner lobes; keels 0.7–1.0 mm. wide, scarcely to strongly prominent, weakly to strongly papillose (under magnification), dark green to purple-tinged; sinistral membrane slightly to strongly curved and bearing few to many blunt processes up to 0.3 mm. long. Corolla pale to deep blue, rarely white, narrowly to broadly funnelform, 25–60 mm. long, 8–15 mm. wide at the orifice, the lobes oblong to obovate-oblong, the tips denticulate to short (1 mm.)-ciliate, the margins with fimbriae to 5 mm. long in the upper half. Stamens included, the filaments inserted in the lower third of the corolla tube, the marginal wings 1.3–3.0 mm. wide at the base, tapering above, strongly incurved; anthers 2–5 mm. long, about 1.5 mm. wide, attached in the upper third; interstaminal glands oval to rounded, prominent and frequently deep green. Pistil sessile to short-stipitate, the gynophore 2–4 mm. long, becoming obscure with age, ovary fusiform, 12–25 mm. long, 2–5 mm. wide; stigmas rounded to flabelliform or reniform, 1–3 mm. wide. Capsule as long as the corolla, dehiscent in the upper third, the tips of the valves slightly recurving. Seeds oblong and angular, light brown, the surface covered with rounded to elongate inflated brown papillae, particularly concentrated at the angles and ends.

North American, extending from the Appalachian Mountains and the Gulf of St. Lawrence in the east to the Great Lakes region and westward across the plains to the Rocky Mountains in Alberta, resolving into several intergrading subspecies apparently of a clinal nature and with numerous minor local variants.

Habitats various according to the subspecies, but in general preferring alkaline areas of about pH 6.7; flowering and fruiting roughly from June to late September; at usually low altitudes from sea-level to a few hundred meters.

Froelich provided an adequate description of *Gentiana crinita* but cited no specimens. In synonymy *Gentiana ciliata* L. (Syst. Pl. 1:645. n. 27) "a var. americana" is given. By "var. americana" Froelich apparently referred to the American element from which Linnaeus drew his description. At this time the problem of selecting a type is deferred because of the difficulty of obtaining certain literature and photographs. Because Fernald<sup>55</sup> interpreted the American portion of the *Gentiana ciliata* L. (Sp. Pl. ed. 2, 334. 1762) to be his *G. victorinii*, the difficulties are increased.

<sup>55</sup> Fernald in *Rhodora* 25:85–89. 1923.

## KEY TO THE SUBSPECIES

- a. Flowers 25–60 mm. long; corolla lobes with lateral fringes 2–5 mm. long in the upper half of the lobe, the tips frequently short-ciliate also; calyx keels 0.1–0.8 mm. broad at the base.
- b. Median leaves ovate to lanceolate-ovate, rounded to subcordate at the base, linear to elliptic only in the small phase. North Carolina to Massachusetts and Maine west to Minnesota and Manitoba.....2a. *G. crinita* ssp. *crinita*
- bb. Median leaves linear to linear-lanceolate. Upper New York through the Great Lakes region to Minnesota and Manitoba.....2b. *G. crinita* ssp. *procera*
- aa. Flowers 10–40 mm. long; corolla lobes with short lateral fringes, the tips dentate or erose, rarely ciliate; calyx keels absent or not prominent.
- c. Flowers 30–35 mm. long; corolla lobes orbicular; style 1.0–1.5 mm. long; stigmas flabelliform. Intercotidal zone of the St. Lawrence River. Quebec.....2c. *G. crinita* ssp. *victorinii*
- cc. Flowers 25–40 mm. long; corolla lobes usually oblong, somewhat truncate; stigmas reniform, sessile. Gaspé, Quebec, and James Bay, southward to North Dakota, westward to Alberta.....2d. *G. crinita* ssp. *macounii*

The subspecies of *G. crinita* overlap in distribution a great deal so that many individual collections at the margins of ranges are difficult to assign. A general clinal condition exists between Alberta and the Appalachians. The eastward extreme has ovate to ovate-lanceolate leaves, long lateral corolla lobe fringes, long corollas, long-papillose seeds, coarsely papillose calyx keels, relatively distinct gynophores, and stems branching in the upper part. The western population consists of slender plants with linear leaves, shorter lateral fringes, small corollas, short seed papillae, less papillose keels, sessile capsules, and the stems branch chiefly from the base. Although no sharp division exists there is a change along certain lines that is useful for separation into subspecies. On the east side of the cline, ssp. *procera* differs from ssp. *crinita* principally in its linear leaves, although the flower characters seem to remain much the same. Other characters change gradually to merge with the plains subspecies. The western ssp. *macounii* is reserved for the short-flowered members, although occasionally long-flowered individuals appear. The key, of course, should be regarded as a guide only.

## 2a. GENTIANELLA CRINITA (Froel.) G. Don, ssp. CRINITA

*Gentiana ciliata* L. Syst. 1:645. 1756, in part, as to American element.

*Gentiana fimbriata* Andr. Bot. Rep. 509. 1808, ex ic.

*Denckea crinita* (Froel.) Raf. in Med. Repos. II. 5:352. 1808.

*Anthopogon incarnatum* Raf. New Fl. N. Am. 4:90. 1836, ex char.

*Anthopogon brevifolium* Raf. loc. cit. 91. 1836, ex char.

*Gentiana crinita* Froel. f. *albina* Fern. in Rhodora 19:152. 1917. (T.: Bergen s. n.!)

In the Appalachians from western North Carolina to Massachusetts and Maine, northwest to eastern Ontario and western Quebec, west to the Great Lakes region, forming a cline with *G. crinita* ssp. *procera* and with ssp. *macounii*, and occurring as far west as Minnesota and Manitoba.

In a variety of habitats: roadsides, clearings in open woods, swampy ground, gravel, sand, railway embankments, and shallow soils over limestone, in general preferring calcareous habitats. In the western part of the range found in open oak woods, on damp prairies, and boggy places; flowering throughout August to early October; fruiting from about mid-September until late October.

## CANADA:

MANITOBA: Ochre River, *Grob s. n.* (DAO); Stony Mountain, *Grob s. n.* (DAO, MO), *Macoun s. n.* (CAN, F); Beausejours, *Schaeffer s. n.* (PH); Burnside, *McMorine s. n.* (DAO); Clear Lake, Riding Mt. Nat. Park, *Jackson 29-18* (DAO); Winnipeg, *Fowler 1* (DAO); Dauphin, *Scoggan 10503* (CAN); Grand Rapids, Lake Winnipeg, *Scoggan 4822* (CAN); Vivian, *Löve 5265* (CAN, JBM).

ONTARIO: Bruce Co.: *Bassett & Mulligan 194* (DAO). Carleton Co.: Britannia, *Macoun s. n.* (CAN, GH); Ottawa, Dow's Swamp, *Gillett 6055* (DAO), *Kellett s. n.* (CAN, DAO, MO); Kinburn, *Gillett 6056* (DAO); Lanark Co. border: *Dore & Gillett 47-1018* (DAO); Harwood Plains, *Dore & Rhodes 12868* (DAO). Elgin Co.: St. Thomas, *Fisher s. n.* (MO). Essex Co.: Turkey Point, Lake Erie, *Soper 759* (DAO). Grenville Co.: Merrickville, *Terrill 53* (DAO). Middlesex Co.: London, *Burgess s. n.* (CAN, DAO). Peterborough Co.: Clarina, Dummer Twp., *Dore & Hammond 14062* (DAO). Stormont Co.: Farran Point, *Dore & Van Rens 15667* (DAO). Waterloo Co.: Galt, *Herriot s. n.* (CAN, DAO); German Mills, *Montgomery 298.39* (DAO). Welland Co.: Niagara Falls, *McCalla 314* (CAN); St. Davids, *Scott 123* (CAN). Wentworth Co.: Hamilton, *Cody 105* (DAO). York Co.: Toronto, *Pennell 13124* (PH).

QUEBEC: Huntingdon Co.: Huntingdon, *Raymond & Kucyniak 2* (DAO, JBM).

## UNITED STATES:

CONNECTICUT: Fairfield Co.: Stratford, *Eames s. n.* (GH). Hartford Co.: Southington, *Bissell 146* (MO). Litchfield Co.: South Canaan, *Greenman 1446* (GH, MO, US). Middlesex Co.: Saybrook, *Kennedy s. n.* (GH). New Haven Co.: New Haven, *Safford 259* (US).

ILLINOIS: Cook Co.: *Babcock s. n.* (US); Chicago, *Blankford s. n.* (F). Lake Co.: Waukegan, *Earle s. n.* (US). Stephenson Co.: Freeport, *Johnson s. n.* (US).

INDIANA: Allen Co.: Lake Everett, *Deam 22064* (GH). La Grange Co.: Ontario, *Deam 15057* (GH). Lake Co.: Clarke, *Lansing 3970* (F, GH). Porter Co.: Dune Park, *Chase 2115* (F, US), *Gillett 6058* (DAO). St. Joseph Co.: Churchill *s. n.* (MO); Chain Lakes, *Nieuwland 11650* (MO, US). Steuben Co.: Graveyard Lake, *Deam s. n.* (MO, US).

IOWA: Allamakee Co.: Postville?, *Schutz 182* (GH). Johnson Co.: Fitzpatrick & Fitzpatrick *s. n.* (F, GH, NY).

MAINE: Cumberland Co.: Falmouth, *Blake s. n.* (PH); Cape Elizabeth, *Gayle 904* (US); South Harpswell, *Keller s. n.* (PH); West Harpswell, *Read 3492* (MO). Kennebec Co.: Litchfield, *Sturtevant s. n.* (MO). Lincoln Co.: Monhegan Island, *Churchill s. n.* (MO). Oxford Co.: Hartford, *Parlin s. n.* (GH). York Co.: Kennebunkport, *Gilbert s. n.* (GH).

MARYLAND: Baltimore Co.: *Gresham s. n.* (US), *Morris s. n.* (PH).

MASSACHUSETTS: Berkshire Co.: Cheshire, *Churchill s. n.* (GH). Hampshire Co.: Worthington, *Rice s. n.* (US). Bristol Co.: Nonquit, *Sturtevant s. n.* (MO). Essex Co.: Bowford, *Murdoch 5264* (F). Franklin Co.: Buckland, *Forbes s. n.* (GH). Hampden Co.: West Granville, *Seymour 362* (GH, MO). Hampshire Co.: Mt. Tom, *Johnson 124* (US). Middlesex Co.: Chelmsford, *Beattie s. n.* (MO); Waverley, *Bergen s. n.* (GH). Norfolk Co.: Canton, *Kennedy s. n.* (GH). Plymouth Co.: Kingston, *Ridler s. n.* (F). Suffolk Co.: Boston, *Faxon & Faxon s. n.* (GH). Worcester Co.: Bolton, *Churchill s. n.* (GH, US).

MICHIGAN: Berrien County: *Millsbaugh 3874* (F). Gratiot Co.: Alma, *Davis s. n.* (US). Jackson Co.: *Camp & Camp s. n.* (F). Midland Co.: Midland, *Dreisbach 5418* (PH). Washtenaw Co.: Geddes, *Farwell 7694* (GH). Wayne Co.: Dearborn, *Chandler s. n.* (US).

MINNESOTA: Clearwater Co.: Mississippi headwaters, *Grant s. n.* (GH, PH). Fillmore & Olmsted Cos.: Chatfield, *Hale s. n.* (PH). Hennepin Co.: Fort Snelling, *Mearns s. n.* (US). Houston Co.: *Freiberg s. n.* (MO). Morrison Co.: *Sandberg 877* (US). Nicollet Co.: St. Peters River, *Geyer s. n.* (MO, US). Todd Co.: Philbrook, *Hotchkiss & Jones 498* (GH). Winona Co.: Stockton, *Holzinger s. n.* (US).

NEW HAMPSHIRE: Belknap Co.: Gilmanton, *Gilbreth s. n.* (GH). Cheshire Co.: Marlboro, *Robmann 373* (GH). Grafton Co.: Franconia, *Kennedy s. n.* (GH). Hillsboro Co.: Pelham, *Knowlton s. n.* (GH). Rockingham Co.: Derry, *Batchelder s. n.* (MO).

NEW JERSEY: Bergen Co.: Tenafly, *Poggenburg s. n.* (GH). Cape May Co.: Ocean View, *Meredith s. n.* (GH). Essex Co.: Verona, *Lighthipe s. n.* (MO). Morris Co.: Lake Hapatcony, *Fisher s. n.* (MO, US). Somerset Co.: Watchung, *Moldenke 7377* (CAN). Sussex Co.: Egypt Mills, *Bartram s. n.* (PH). Union Co.: Summit, *Parker s. n.* (GH).

NEW YORK: Albany Co.: Albany, *Beck s. n.* (NY). Broome Co.: Glenwood Ravine, *Millsbaugh s. n.* (F). Columbia Co.: Canaan, *Harrison 11* (US). Dutchess Co.: Clove, *Standley & Bollmann 12365* (US). Erie Co.: Buffalo, *Clinton s. n.* (PH). Jefferson Co.: Watertown, *Keyes s. n.* (US). Madison Co.: Merrillville, *House 26205* (GH). Monroe Co.: Irondequoit Valley, *Riley 7018* (GH). Niagara Co.: Cascadilla Creek, *Townsend s. n.* (WS). Ontario Co.: Geneva, *Wing s. n.* (MO). Orange Co.: Black Rock Forest, *Raup 7949* (GH). Richmond Co.: Staten Island, Richmond West, *Dowell 4285* (MO). St. Lawrence Co.: Oswegatchie, *Phelps 776* (GH, US). Suffolk Co.: River Head, *Miller s. n.* (US). Tompkins Co.: Fall Creek below Varna, *Eames & MacDaniels 4827* (GH). Washington Co.: Tripoli, West Fort Ann, *Burnham s. n.* (GH). Westchester Co.: Lake Mohegan, *Pennell 9328* (PH).

NORTH CAROLINA: Macon Co.: Nantahala Mountains, *Huger s. n.* (NY).

OHIO: Erie Co.: Milan Township, *Moseley s. n.* (F). Lucas Co.: *Pontius & Bartley 1006* (US).

PENNSYLVANIA: Berks Co.: *Small s. n.* (F). Bucks Co.: Bridgeton, *Bright 11036* (WS). Centre Co.: Scotia, *Kelly & Kelly s. n.* (GH). Chester Co.: *Rothrock s. n.* (F). Delaware Co.: *MacElwee 1468* (GH). Erie Co.: Presque Isle, *Garber s. n.* (PH). Huntingdon Co.: Whipple Dam, *Wahl 1170* (GH, US). Lancaster Co.: Dillerville, *Long 33914* (GH). Luzerne Co.: Wilkes-Barre, *Thurston s. n.* (US). Monroe Co.: Pocono Summit, *Small s. n.* (F, PH). Montgomery Co.: Greenlane, *Shaeffer 279* (GH). Northampton Co.: Flowertown, *Dowell 1014* (US). Philadelphia Co.: Wissahickon, *James s. n.* (GH). York Co.: Loganville, *Glatfelter 349* (MO). Wyoming Co.: Osterhout, *Glowneke 9370* (GH).

RHODE ISLAND: Providence Co.: East Providence, *Reynolds 0656* (GH).

VERMONT: Bennington Co.: Shaftsbury, *Knowlton s. n.* (PH). Rutland Co.: West Rutland, *Eggleston s. n.* (GH); Ira, *Eggleston s. n.* (F). Windham Co.: Whittingham, *St. John 421* (PH, US).

WEST VIRGINIA: Greenbrier Co.: Lewisburg, *Franklin s. n.* (GH).

WISCONSIN: Brown Co.: Fort Howard, *Shuette s. n.* (F, GH). Crawford Co.: Prairie du Chien, *Hale s. n.* (MO). Monroe Co.: Sparta, *Palmer 28466* (MO). Racine Co.: Racine, *Davis s. n.* (GH). Sawyer Co.: Hayward, *Gilbert & Gilbert s. n.* (GH). Walworth Co.: Lake Geneva, *Blatchford s. n.* (F).

Because *G. crinita* ssp. *crinita* has been observed and collected in the field, a brief description of its habitat and mode of growth is introduced here.

During September, 1951, a small colony near the village of Kinburn, Carleton County, Ontario, about 20 miles west of Ottawa, was kept under observation. The colony was restricted to an area about one-eighth of a mile long and a few hundred yards wide, and was further restricted to shallow soil over limestone. Plants were rather abundant, and grew in open *Thuja occidentalis*-*Populus tremuloides* woods. *Halenia deflexa* also was found here but was restricted to a slightly drier microhabitat situated in clearings in *Thuja* woods. This microhabitat was termed a "cedar glade" in contrast to the more open and wetter habitat of *G. crinita*.

In direct sunlight, corolla lobes of *G. crinita* were observed to spread at an angle of about 45° but were closed in shaded places. The color of the lobes varied from a purple-blue to slightly reddish. The only insects observed about the flowers were a few ants and flies although thrips were found within the corollas.

The frequency and distribution of small, depauperate individuals within this population were of particular interest; for such plants had not only been observed on herbarium sheets, but had been deliberately selected out and described as forms and varieties by early authors. These small plants are about 5–20 cm. tall, and usually bear a single flower considerably smaller than those of the well-developed individuals. Moreover, in comparison with well-developed plants, the leaves are smaller and elliptic rather than ovate. In our colony, small plants were scattered among larger plants without any apparent preference to microhabitat. No definite explanation can be given at this time for the occurrence of these plants, but it is suggested that they are seedlings produced by early-flowering individuals during the same year. They are of interest, too, because they also occur in populations of other taxa in various parts of the continent. Large numbers of them were seen in Yellowstone Park, Wyoming, interspersed within a population of *G. detonsa* ssp. *elegans*, particularly.

In an effort to determine their life span, large plants from this colony were tagged and observed again the following year. In this region they prove to be annuals. No over-wintering rosettes were observed.

2b. *GENTIANELLA CRINITA* (Froel.) G. Don, ssp. *procera* (Th. Holm) J. M. Gillett, comb. & stat. nov.

*Gentiana barbata*  $\beta$  *Browniana* Hook. ex Macnab, in Edinb. New Phil. Jour. 19:62. 1835. (T.: Macnab s. n., photo MO!).

*Anthopogon virgatum* Raf. Fl. Tellur. 3:25. 1837, ex char.

*Gentiana procera* Th. Holm, in Ottawa Nat. 15:111. 1901. (T.: Dodge s. n.!).

*Anthopogon procerus* (Th. Holm) Rydb. in Brittonia 1:94. 1931.

*Gentianella procera* (Th. Holm) Hiit. in Mem. Soc. Faun. Fl. Fenn, no. 25:77. 1950.

From upper New York through the Great Lakes region to Minnesota, North Dakota and Manitoba. Clinal in nature, closely resembling ssp. *crinita* in the eastern part of the range except for the narrower leaves, approaching ssp. *macounii* in the western part, with shorter cilia, more linear leaves, lax habit and smaller seed papillae. In the western part including those individuals with coarse stems and large flowers.

CANADA:

MANITOBA: Aweme, *Criddle* s. n. (DAO, MO); Bird's Hill, Winnipeg, *Denike* 1759 (DAO); Ciento, *Dore* 9196 (DAO); Carroll, *Senn & Gordon* 3129 (DAO); Ochre River, *Scoggan* 10508 (CAN); Stony Mountain, *Macoun* s. n. (CAN, F).

ONTARIO: Bruce Co.: Hay Bay, *Krotkov* 7212 (GH). Gray Co.: Craigleith, *Victorin & Germain* 49464 (GH, MO, US, WS). Huron Co.: Banks of the Maitland River, *Macnab* s. n. (BM, PH). Lambton Co.: near Sarnia, *Dodge* s. n. (TYPE, CAN), *Dodge* 7082 (MO); Sarnia, *Macoun* s. n. (CAN). Manitoulin Dist.: Manitoulin Is., *Sims* s. n. (DAO); Wolsley Lake, *Thompson* s. n. (UBC); Fishing Is., Lake Huron, *Macoun* s. n. (CAN); Whitefish Is., *Macoun* s. n. (CAN); Cockburn Is., Boom Pt., *Grassl* 400 (NY); Centre Is., *Ogden* 2395 (US); Manitowaning Is., *Ogden* 2428 (US); Johnstones Harbour, *Macoun* s. n. (CAN). Simcoe Co.: Collingwood, *Victorin, Rolland & Meilleur* 45073 (DAO, GH). Waterloo Co.: Galt, *Herriot* s. n. (DAO, MO).

UNITED STATES:

ILLINOIS: Cook Co.: *Babcock* s. n. (MO). Du Page Co.: *Moffatt* 508 (GH). Kane & Cook Cos.: Elgin, *Sherff* 1986 (MO). Kane Co.: Kankakee, *Greenman* 3538 (MO).



Lake Co.: Waukegan, *Smith 6050* (GH, MO). McHenry Co.: Ringwood, *Vasey s. n.* (PH). McLean Co.: Normal, *Vasey s. n.* (GH). Winnebago Co.: Fountaindale, *Bebb s. n.* (NY, PH).

INDIANA: Fulton Co.: Bruce Lake, *Deam 46341* (GH). Kosciusko Co.: Chapman Lake, *Friesner 23145* (DAO, WS). Lake Co.: Pine, *Chase s. n.* (GH). La Porte Co.: Mill Creek, *Friesner 14190* (NY). Marshall Co.: Lake Maxinkuckee, *Scovell & Clark 1436* (US). St. Joseph Co.: Chain Lake, *Nieuwland 11642* (MO). Wayne Co.: Webster's Crossing, *Nieuwland s. n.* (US).

IOWA: Cerro Gordo Co.: Mason City, *Shimek s. n.* (MO). Dickinson Co.: West Okoboji Lake, *Shimek s. n.* (GH, MO, US, WS). Emmet Co.: *Cratty s. n.* (PH). Palo Alto Co.: 5 mi. e. Ruthven, *Hayden 10191* (GH, MO, NY). Winneshiek Co.: Fremont Twp., *Shimek s. n.* (MO).

MICHIGAN: Alpena Co.: Alpena Point, Lake Huron, *Cain, Raymond & Kucyniak 936, 943* (JBM). Calhoun Co.: Albion, *Barr s. n.* (F). Charlevoix Co.: Beaver Island, Lake Michigan, *Gillman s. n.* (NY). Cheboygan Co.: Mackinaw City, *Hermann 7311* (F, MO, US, WS). Emmet Co.: Wilderness State Park, *Cain, Raymond & Kucyniak 600* (JBM). Ionia Co.: Hubbardston, *Wheeler s. n.* (US). Kalamazoo Co.: Lyons Lake, *Kenoyer 278* (F). Kent Co.: Grand Rapids, *Crozier s. n.* (US). Mackinac Co.: Scotty Bay, Lake Huron, *Eblers 4905* (F, US). Oakland Co.: Orian Twp., *Chandler s. n.* (US). Schoolcraft Co.: Manistique, *Cain, Raymond & Kucyniak 565* (DAO, JBM). St. Clair Co.: Port Huron, *Dodge s. n.* (NY). Washtenaw Co.: Cavanaugh Lake, *Grassl 7745* (MO). Wayne Co.: Detroit, *Schott s. n.* (F).

MINNESOTA: Cass Co.: Big Thunder Lake, *Richards 356* (F). Clay Co.: Muskoda, *Ballard 3064* (GH). Clearwater Co.: Itasca Park, *Grant 3362* (GH, MO, US). Dakota Co.: Nichols, *Rosendahl 4757* (F). Hennepin Co.: Fort Snelling, *Mearns s. n.* (US). Ottertail Co.: Richdale, *Chandonnet s. n.* (MO). Pope Co.: Glenwood, *Taylor s. n.* (PH). Ramsey Co.: St. Paul, *Sheldon s. n.* (GH, WS). Stearns Co.: St. Cloud, *Dewart s. n.* (MO). Winona Co.: Winona, *Holzinger s. n.* (US).

NEW YORK: Monroe Co.: Genesee River, *Eaton s. n.* (NY). Niagara Co.: Niagara Falls, *Canby s. n.* (NY); Goat Island, Niagara, *Engelmann s. n.* (MO). St. Lawrence Co.: Pollys Creek, *Muenschler & Maguire 1315* (GH).

NORTH DAKOTA: Ransom Co.: Anselm, *Stevens 227* (F).

OHIO: Champaign Co.: Urbana, *McFarland 4507* (US). Clark Co.: Tremont City, *Leonard 2018* (US). Pickaway Co.: Deer Creek, nr. Williamsport, *Collector unknown* (NY). Ross Co.: Kingston, *Bartley & Pontius 766* (NY).

WISCONSIN: Brown Co.: Fort Howard, *Schuetz s. n.* (US). Dane Co.: Madison, *Hedde 953* (F). Door Co.: Bailey's Harbour, *Fassett et al. 14825* (GH). Milwaukee Co.: *Lapham s. n.* (DAO, GH, MO). Racine Co.: *Hasse s. n.* (NY). Waukesha Co.: Delafield, *Larrabee s. n.* (GH).

2c. GENTIANELLA CRINITA (Froel.) G. Don, ssp. *victorinii* (Fern.) J. M. Gillett, comb. & stat. nov.

*Gentiana victorinii* Fern. in *Rhodora* 25:87. 1923. (T.: *Victorin 16073!*)

Quebec, restricted to the intercotidal zone of the St. Lawrence River from Deschambault to St. Jean Port Joli; flowering from late July through August until early September; fruiting from mid-August until mid-September.

CANADA:

QUEBEC: Bellechasse Co.: Berthier, *Fernald 2536* (CAN, GH); Beaumont, *Victorin & Rolland 43667* (DAO); St. Vallier, *Victorin, Rolland & Meilleur 45546* (GH). Levis Co.: Levis, *Collector unknown* (DAO); St. Romauld, *Victorin, Rolland & Meilleur 1338* (JBM). L'Islet Co.: St. Jean Port Joli, *Desmarais 1013* (JBM), *Calder 1384* (DAO). Mont-Lotbinière Co.: St. Antoine-de-Tilly, *Victorin, Rolland & Jacques 33696* (CAN). Montmagny Co.: Grosse-Île, *Rousseau 21057* (GH), Berthier en Bas, *Victorin, Boivin, Raymond & Kucyniak 3726* (MO, WS), *Rousseau 21050* (CAN). Montmorency Co.: Ile

d'Orleans, Sainte-Petronille, *Victorin & Rolland 49500* (GH), *Gillett & Van Rens 9704* (DAO); St. Laurent d'Orleans, *Gillett & Van Rens 9722*, St. Jean, *Gillett & Van Rens 9723*, eastern end of Ile d'Orleans, *Gillett & Van Rens 9724* (all DAO). Portneuf Co.: Deschambault, *Gillett & Van Rens 9668* (DAO); Neuville, *Gillett & Van Rens 9693* (DAO); Saint-Augustin, *Victorin, Rolland & Jacques 33868* (GH). Quebec Co.: Cap Rouge, *Victorin 16073* (GH, JBM), *Gillett & Van Rens 9696* (DAO), *Victorin, Boivin, Raymond & Kucyniak 3704* (CAN, DAO, GH, MO, WS). And many more sheets from the same or near-by localities.

One of the most distinctive features of this subspecies is its unique habitat described in such detail by Raymond<sup>56</sup> and Rousseau.<sup>57</sup> During the summer of 1955 a visit was made by the author to this area. Both sides of the St. Lawrence were visited and a circuit made of l'Île d'Orléans. From my observations it is suspected that the plants are annuals although Raymond cautiously writes: "Toutes ces espèces sont annuelles ou bisannuelles." The water throughout the range is fresh but may be salt in the eastern part following persistent east winds. As a result of daily flooding by the tide, the plants usually are covered with debris or a film of mud. A cline in flowering time was observed extending downstream from Deschambault on the north shore to Berthier and Montmagny on the south shore where the plants were in fruit only. The small phase seen in other populations occurs here also but is less common.

Subspecies *victorinii* is morphologically somewhat intermediate between ssp. *procera* and ssp. *macounii* and may be considered as a possible ecological nothomorph stemming from the *macounii-procera-crinita* cline.

2d. GENTIANELLA CRINITA (Froel.) G. Don, ssp. *macounii* (Th. Holm) J. M. Gillett, comb. & stat. nov.

*Gentiana macounii* Th. Holm, in *Ottawa Nat.* 15:110. 1901. (T.: *Macoun s. n.!*)

*Gentiana detonsa* Rottb. var. *tonsa* Lunell, in *Bull. Leeds Herb.* 2:7. 1908. (T.: *Lunell s. n.!*)

*Anthopogon tonsum* (Lunell) Rydb. in *Bull. Torr. Bot. Club* 40:463. 1913.

*Anthopogon macounii* (Th. Holm) Rydb. loc. cit. 463. 1913.

*Anthopogon procerum* Lunell (incorrectly attributed to Th. Holm by Lunell), var. *tonsum* Lunell, in *Am. Midl. Nat.* 4:507. 1916. (T.: *Lunell s. n.!*)

*Anthopogon procerum* var. *tonsum* Lunell f. *uniflorum* Lunell, loc. cit. 1916. (T.: *Lunell s. n.!*)

*Gentiana gaspensis* Vict. in *Contr. Lab. Bot. Univ. Montréal* 20:10. 1932. (T.: *Victorin, Rolland & Jacques 33751!*)

*Gentiana tonsa* (Lunell) Vict. loc. cit. 14. 1932.

Alberta, Saskatchewan, and Manitoba, southern James Bay, and in Gaspé, Quebec; southward in the Great Plains through North Dakota and Minnesota and transitional to *G. crinita* ssp. *procera* west of the Great Lakes.

About the margins of sloughs and along river banks and meadows, occasionally in sandy swales and calcareous bogs. Flowering from late June to late August, fruiting during August and into September.

<sup>56</sup> Raymond, M., in *Nat. Canad.* 78:81-87. 1951.

<sup>57</sup> Rousseau, J., in *Contrib. Lab. Bot. Univ. Montréal* 23:1-7. 1932.

## CANADA:

ALBERTA: Lees Creek, Cardston, *Macoun s. n.* (CAN, TYPE); Fort Pitt, Saskatchewan River, *Macoun s. n.* (CAN); Banff, *Macoun s. n.* (GH, MO), *McCalla 2175* (NY, US), *Sanson in 1899*, *Fletcher in 1898* (CAN); Red Deer, *Grospe (?)* (WS); Calgary, *Turner 3759* (CAN); Shaganappi, *Moodie 44* (F, NY); Jasper, *Scamman 3357* (GH); Grattan Creek, *Macoun & Herriot s. n.* (CAN, NY); Blindman River, *Budd 1839* (SWC); Bow River, *Macoun s. n.* (CAN, US); Fort Saskatchewan, *Turner 2720* (CAN, DAO); Edmonton, *Moss 2412* (GH); Macleod North, *Dixon 1533* (DAO); Lacombe, *Lindsay & Leggett 339* (DAO).

BRITISH COLUMBIA: Field, *Macoun s. n.* (CAN, NY).

MANITOBA: Aweme, *Criddle s. n.* (DAO); Bird's Hill, Winnipeg, *Denike 1567* (DAO); Grand Rapids, Lake Winnipeg, *Scoggan 4854* (CAN); Beulah, *Dennis s. n.* (DAO); Ochre River, *Grob s. n.* (DAO); Little Saskatchewan River, *Scoggan 4942* (CAN); Lake Winnipegosis to Cedar Lake, *Scoggan 4639* (CAN); Verden, *Grob s. n.* (DAO); Stony Mountain, *Macoun s. n.* (F); Duck Mt., *Halliday 90* (CAN); Broomhill, *Senn & Gordon 3116* (DAO); Shoal Lake, *Garton 3165* (CAN); Bellhampton, *Bolton s. n.* (SWC).

ONTARIO: Albany, James Bay, *Dutilly & Lepage 16224* (CAN, DAO, US); Moose Factory to Rupert House, *Drexler s. n.* (GH); Albany, *Lepage 30245* (CAN, JBM); Delta of Albany River, *Jobansen 30* (CAN), *Spreadborough s. n.* (CAN); Moose River, Renison, Mile 156, *Hustich & Tuomikoski 24* (CAN); Attawapiskat, *Dutilly & Lepage 16355* (CAN).

QUEBEC: James Bay: Rupert House, *Macoun s. n.* (CAN). Bonaventure Co.: Bonaventure River, *Kucyniak, Victorin, Boivin & Raymond 4008* (CAN, DAO, GH, MO, US, WS), *Marie-Victorin et al. 33751* (CAN, GH, JBM, NY), *Scoggan 1231, 981* (CAN), *Raymond & Kucyniak 1939* (CAN).

SASKATCHEWAN: McKague, *Breitung s. n.* (DAO); Nipawin, *Breitung 5998* (DAO, MO), *354* (CAN); South Saskatchewan River, *Boivin & Breitung 6700* (DAO); Rose Valley, *Dubreuil s. n.* (DAO); Canora, *Carmichael 189* (DAO); Prince Albert, *Fraser s. n.* (DAO); Tramping Lake, *Macoun & Herriot s. n.* (GH, NY, MO); Algrove, *Ledingham & Russell 1365* (DAO); Sutherland, *Russell s. n.* (DAO); Whitewood, *Tinline & Russell 53922* (DAO); Riwei Hills Reserve, *Rowe 442* (DAO); Pike Lake, *Russell s. n.* (DAO); Saskatoon, *Fraser s. n.* (SWC); Elbow, *Campbell s. n.* (SWC), Cut Knife, *Campbell s. n.* (SWC); St. Louis, *Senn, Grob & Russell 2843* (DAO); Carleton House to Bear Lake, *Richardson s. n.* (GH); Prongua, *Mead & Russell 51235* (DAO); Beasant, Moose Jaw District, *Hudson 570* (DAO); Blackfoot Crossing, Bow River, *Macoun s. n.* (CAN).

## UNITED STATES:

MONTANA: Teton River, *Scribner 154* (GH, PH, US).

NORTH DAKOTA: Benson Co.: Butte, *Lunell s. n.* (MIN, MO, NY, US). McHenry Co.: Towner, *Lunell s. n.* (MIN); Wright *s. n.* (NY). Rolette Co.: Gravel Lake, *Mabbott 485* (US).

*Gentiana gaspensis* has been included within *ssp. macounii* since the differences are such that they easily come within the range of variation of the remainder of the population. The Gaspé specimens have slightly smaller flowers and branch from the base. However, nearly identical material occurs along the southern shore of James Bay, although I lack the habitat data necessary to ascertain whether it is confined to the same brackish meadow habitat as in the Gaspé plants. One or two collections from Manitoba also are exceedingly difficult to separate from the Quebec specimens. The occurrence of such plants seems to provide further evidence of a link with the western prairie population.<sup>58</sup>

<sup>58</sup> Some material from James Bay nears *G. detonsa* in gross morphology but the papillose calyx keel versus the smooth keel separates all but a few sheets examined. Still I feel that the papillose-keeled fringed gentians and the smooth-keeled group form two natural divisions that should be maintained at the specific level at least for the present.

Although the type collection of subspecies *macounii* comes from Cardston, Alberta, it is not typical of the majority of the population. Alberta material is more frequently branched from the lower part than Saskatchewan and Manitoba material. This characteristic must be considered a local variant within the population as a whole since other characters either are identical or come within the variation range of the subspecies.

3. *GENTIANELLA barbellata* (Engelm.) J. M. Gillett, comb. nov.

*Gentiana barbellata* Engelm. in Trans. Acad. Sci. St. Louis 2:216. 1862. (T.: Parry 208!)

*Gentiana moseleyi* A. Nels. in Bot. Gaz. 31:396. 1901. (T.: Moseley A.293!)

*Anthopogon barbellatus* (Engelm.) Rydb. in Bull. Torr. Bot. Club 33:148. 1906.

Acaulescent or caulescent perennials 5–15 cm. tall, from slender, fleshy, branched, horizontal rhizomes, the rhizome branches erect, 5–10 cm. long, becoming thickened towards the surface. Basal leaves oblanceolate, rarely linear, rounded or obtuse, gradually attenuate below, expanded and connate to clasping at the base, forming a membranaceous sheath enclosing the ends of the rhizome, 1.5–9.0 cm. long, 0.3–1.2 cm. wide; median leaves oblanceolate to linear, obtuse or rarely acute, attenuate to about the width of the stem at the base, connate or clasping, 2–6 cm. long, 0.5–1.0 cm. wide. Flowers solitary and terminal, sessile or short-pedicellate, the pedicels to 5 mm. long, or axillary at the node immediately beneath, the axillary flowers sessile or short-pedicellate, the pedicels 1–2 cm. long; terminal flower (and occasionally the axillary flowers) subtended by a pair of frequently colored, hyaline-margined, lanceolate to linear, bract-like leaves. Calyx funnelform, 11–25 mm. long, 5–10 mm. wide at the orifice; lobes triangular to lanceolate, equal, as long as or shorter than the tube, somewhat crispate near the acute tips, 2–5 mm. wide at the base; sinuses acute, covered on the inside by a small membrane bearing 1–6 minute blunt processes 0.5 mm. long. Corolla deep blue, greenish yellow within, narrow funnelform, 24–45 mm. long, 5–10 mm. wide; lobes oblong with obtuse to acute erose tips, spreading in flower, irregularly crumpled and persistent in fruit, as long as the tube or longer, 15–25 mm. long, 2–6 mm. wide, the lateral margins with setae 1–2 mm. long in the lower half, entire to dentate in the upper. Stamens slightly exserted; filaments inserted above the middle of the corolla tube, the barely incurved marginal wings 0.5 mm. wide at the base, tapering gradually above; anthers oval, 2 mm. long, 1.5 mm. wide. Pistil stipitate, the gynophore 4–5 mm. long; ovary ellipsoid, sharply attenuate at the base, 10 mm. long, 3 mm. wide; stigmas sessile, elliptical, 2 mm. wide. Mature capsule as long as the corolla tube, dehiscent in the upper third, the tips of the valves erect. Seeds somewhat obovoid, papillose.

Central Colorado; Wyoming in Sublette, Teton and Carbon counties in the Medicine Bow Range; Utah in the La Sal Mountains; New Mexico in Colfax, Taos and Rio Arriba counties; Arizona in the San Francisco Mountains; at elevations of 1,000–3,600 meters; on rocky, alpine and subalpine slopes, below timber line in

open coniferous forest, and occasionally in open wet meadows; flowering from mid-August until late September, fruiting from mid-September until snowfall.

UNITED STATES:

ARIZONA: Coconino Co.: San Francisco Mountains, *Knowlton 126* (US).

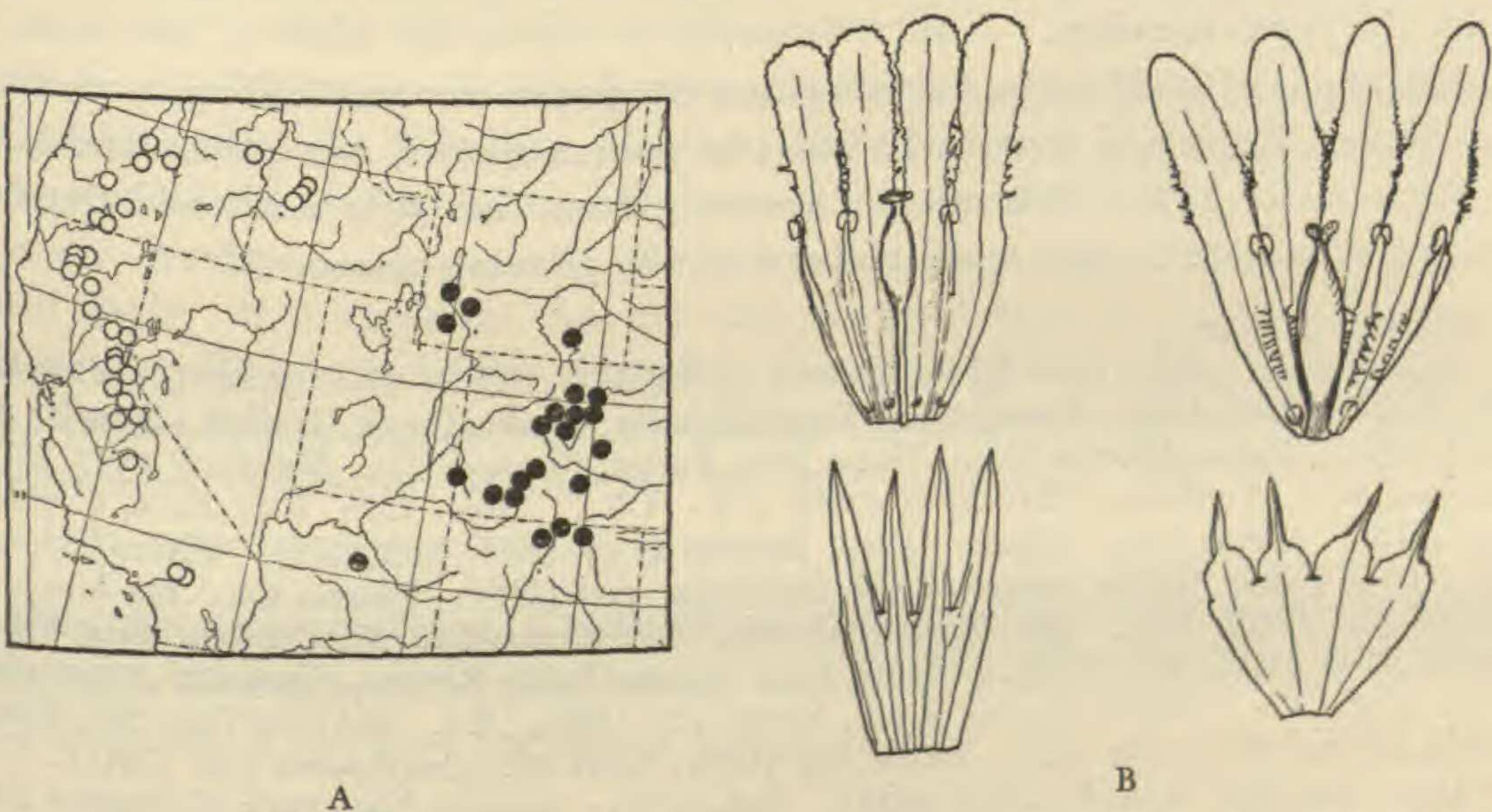
COLORADO: Boulder Co.: *Moseley A.293* (RM). Clear Creek Co.: Berthoud's Pass, *Engelmann s. n.* (F, MO); Gray's Peak, *Patterson 94* (GH, MO, NY, US), *Rydberg 2793* (NY), *Jones 800* (NY), *Snow s. n.* (F). Custer Co.: Sangre de Cristo Mts. near Westcliffe, *Eggleston 6316* (US). El Paso Co.: Gentian Dell, *Clements & Clements 214* (GH, MO, NY, US). Gunnison Co.: Taylor River, *Coulter s. n.* (US). Jefferson Co.: Smith Horn, *Greene 327* (GH). Lake Co. Twin Lakes, *Wolf & Rothrock 794* (GH, US). Larimer Co.: Mount Flora, Snowy Range, *Parry 208* (MO, US); Estes Park, *Clokey 3832* (NY). Mineral Co.: Wagon Wheel Gap, *Murdock 4876* (F, MO). Park Co.: Leadville Forest, *Eggleston 11975* (US); Mt. Harvard, *Clements 409* (NY). Saguache Co.: *Weber 3598* (WS). San Miguel Co.: Wilson, *Mason s. n.* (NY); Breckenridge, *Brandege 253* (MO, NY); Pike's Peak, *Underwood s. n.* (NY). Location unknown: *Parry in 1872* (NY), *in 1873* (F), *Parry 440* (F).

NEW MEXICO: Colfax Co.: Baldy Peak, *Standley 14343* (US). Taos Co.: Costillo Pass, *Howell 200* (US).

UTAH: Grand Co.: Stenize Stellen, La Sal Mts., *Purpus 7032* (MO, US). Sanpete Co.: Summit of Heliotrope, above Mayfield, *Collector unknown* (NY).

WYOMING: Carbon Co.: Medicine Bow Mts., *Nelson & Nelson 1138* (MO, NY). Sublette Co.: Green River Lakes, Wind River Mts., Mutulse Creek, *Griffiths s. n.* (NY); Cliff Creek, *Curtis s. n.* (NY), *Ownbey 1129* (MO, WS); 25 mi. w. Big Piney, above Middle Piney Lake, *Meyer & Meyer 2365* (NY). Teton Co.: Crystal Creek Divide, *Murie 1052* (MO).

*Gentianella barbellata* is the only perennial species of the genus in North America. The flowers bear unique rows of cilia below the staminal insertion, somewhat comparable to the substaminal cilia in the related European perennial *Gentianella ciliata* (L.) Börner. The latter has caudate seeds, however, while in *G. barbellata* the seeds are papillose and ecaudate.



A

B

Fig. 2. A, distribution of *Gentianella simplex* (circles) and of *G. barbellata* (black dots). B, calyx and corolla of *G. simplex* (left), actual size, and of *G. barbellata* (right),  $\times$  about  $\frac{7}{8}$ .

4. *GENTIANELLA simplex* (A. Gray) J. M. Gillett, comb. nov.

*Gentiana simplex* A. Gray in Newberry, Bot. Rept. U.S. Pac. R.R. Surv. 63:87. 1857. (T.:  
Newberry s. n.!)

*Anthopogon simplex* (A. Gray) Rydb. Fl. Rocky Mts. 659. 1917.

Annuals, 5–35 cm. tall; stems simple, smooth or finely striate. Leaves in 2–6 pairs, somewhat fleshy, the basal leaves spatulate, soon withering, 5–15 mm. long, 1–6 mm. wide, the apex rounded to obtuse, the base connate, the median and upper leaves elliptic, ovate, or lanceolate, 5–20 mm. long, 2–5 mm. wide, the apex obtuse, the base clasping to connate, slightly decurrent. Flowers solitary, terminal on pedicels 2–15 cm. long. Calyx narrowly funnelform, 10–25 mm. long, 5–10 mm. wide at the sinuses; lobes equal, as long as the frequently crispate tube, 5–12 mm. long, 2–5 mm. wide at the base, the outer foliaceous and veiny, occasionally crispate, the inner foliaceous or frequently strongly crispate and recurved; sinuses acute, covered within by a small entire membrane. Corolla pale blue to violet, narrowly funnelform, 20–40 mm. long, 4–10 mm. wide at the orifice; lobes broadly spatulate with rounded to obtuse, erose to dentate tips, erect to slightly spreading at anthesis, 5–15 mm. long, 3–6 mm. wide; sinuses acute, the lateral margins entire or with a few fringes 0.5–1.0 mm. long. Stamens included; filaments inserted in the middle of the corolla tube, the flat to slightly incurved marginal wings 1.5 mm. wide at the base, tapering slightly above; anthers 2 mm. long and wide, attached in the upper third; interstaminal glands elongate, swollen, attached 1 mm. from the base of the tube. Pistil stipitate, the gynophore 7 mm. long; ovary ovate, sharply attenuate at the base, 12 mm. long, 6 mm. wide; stigmas sessile, laminate and minutely lobed, 4 mm. wide. Mature capsule slightly exceeded by the persistent corolla lobes, dehiscing for one-third to half its length, the tips barely parted. Seeds elongate, caudate at both ends, 0.5–1.0 mm. long, 0.01 mm. wide, the body ovoid, the testa reticulate.

Mountains of southern and southeastern Oregon to eastern California, northern and western Idaho and western Nevada; in open meadows, wet places, and bogs; at elevations of 1200–3000 meters; flowering from late July until mid-October; fruiting from late August until the end of the growing season.

## UNITED STATES:

CALIFORNIA: Alpine Co.: Spurs, Hansen 708 (MO). Butte Co.: Jonesville, Copeland 440 (F, GH, MO, US). Fresno Co.: Sierra Nevada, Dinky Creek, Hall & Chandler 570 (MO, US). Lassen-Plumas Cos.: Sierra Nat. Forest, Shuteye Mt., Murdoch 2537 (US). Mariposa Co.: Yosemite, Chesnut & Drew s. n. (US). Mono Co.: Bast Lake, Copeland s. n. (US). Placer Co.: Squaw Valley, Brewer 2153 (GH, MO, US). Placer-Eldorado Cos.: Lake Tahoe Region, Angora Lake, McGregor 210 (US). Plumas Co.: Big Meadows, Austin 488 (MO, US). San Bernardino Co.: San Bernardino Mts., Little Bear Valley, Parish 1659 (GH, MO, WS). Shasta Co.: Lassen Butte Region, Eastwood 1890 (GH, US). Sierra Co.: Little Truckee River, Sonne 218 (MO, US). Siskiyou Co.: Mt. Shasta, Cooke 17810 (WS); Mt. Eddy, Smith 554 (US); Scott Mt., Engelmann s. n. (MO). Trinity Co.: Carrville, Howell 12755 (GH). Tulare Co.: Sequoia Nat. Park, Cronquist 2182 (MO). Tuolumne Co.: Yosemite Nat. Park, Van Schaack & Freytag 3055 (MO). IDAHO: Boise Co.: Stanley, Cronquist 3661 (GH, MO); Stanley Lake, Christ s. n. (ID). Boise National Forest, Gillett, Senn & Frankton 6045 (DAO). Custer Co.:

Stanley Lake, Challis Nat. Forest, *Thompson 13971* (GH, MO, US); Cape Horn, *Macbride & Payson 3638* (GH, MO, US).

NEVADA: Washoe Co.: Incline, Lake Tahoe, *Mason 12208* (CAN, F, GH, MO, US, WS), *Archer 6714* (NY).

OREGON: Baker Co.: Eagle Creek Meadows, *Cusick 2336* (GH, MO, US, WS). Crook Co.: Ochoco Nat. Forest, *Munson & Bray 194* (WS). Deschutes Co.: Deschutes River, Tumalo Village, *Whited 548* (WS). Douglas Co.: Diamond Lake, *Coville & Applegate 460* (US). Klamath Co.: Lake of the Woods, *Applegate 321* (GH); Upper Klamath Lake, *Newberry s. n.* (MO). Umatilla Co.: *Mottet & Peterson s. n.* (ID)

A very distinct species. The height of this handsome plant is rather variable. Apparently this variability depends on the dryness of the habitat and on the nature of the surrounding vegetation. The living plant has been observed in the field in Boise National Forest, Idaho. Here, hundreds of plants in all stages of development grew in damp sandy ground among sedges and among scattered seedling pines. The plants were checked carefully for any deviation from the unbranched habit, and none was found. No insect visitors were seen about the plants, but dissections of several corollas revealed the presence of thrips. *Gentiana calyosa* growing near by was visited by both bees and humming birds.

*Gentianella simplex* may be related to *G. ciliata* of Europe. The caudate seeds of the two species are almost indistinguishable, and are unique among the fringed gentians. *G. ciliata*, however, is reported to be a perennial.

#### DOUBTFUL SPECIES

*GENTIANA VENTRICOSA* Griseb. Gen. & Sp. Gent. 259. 1839, is figured in Hooker's 'Flora Boreali-Americana' and may prove to be of considerable cytological interest. I am assured by Dr. N. Y. Sandwith that no photograph of the type specimen (*Drummond s. n.*, K: "ad cataractas fl. Saskatchewan terrarum Hudsons Bay") could add much to Grisebach's plate. Recently Dr. H. Scoggan of the National Museum of Canada collected another specimen of the same aspect at Grand Rapids, Lake Winnipeg, Manitoba (*Scoggan 4407*, Aug. 6, 1948, CAN!). These specimens have the ovary and stamens shorter than normal and the corolla is poorly developed. Apparently they do not form a large population but are found singly. It is suggested that the two polyploid series of different base numbers occasionally may hybridize to produce this sterile hybrid. That both Scoggan's and Drummond's specimens were collected in essentially the same region seems to indicate some cytological explanation for their occurrence. No similar oddities have been reported elsewhere in the group.

*GENTIANA CRINITA* Froel.  $\beta$  *CERVANTESII* Griseb. in DC. Prod. 9. 102. 1845—The type, a Cervantes collection, has not been located and the description of this Mexican entity is too brief for proper interpretation.

## SUBGENUS II. GENTIANELLA

*Gentiana* L. subgen. *Gentianella* (Moench) Kusnez. in Engl. & Prantl, Nat. Pflanzenfam. ed. 1, 4<sup>2</sup>:85. 1895.

## SECTION AMARELLA (Gaudin, ex Griseb.) J. M. Gillett, comb. nov.

*Gentiana* § *Amarella* Gaudin, ex Griseb. Gen. & Sp. Gent. 238. 1839.

Flowers 4- to 5-merous, small. Calyx lobes with green margins, rarely reduced to teeth; sinuses without an inner membrane. Corolla 4- to 5-, rarely 6- to 8-parted, the lobes ovate, triangular or oblong, entire, the orifice with or without vascularized fimbriae, interstaminal glands epipetalous, and solitary. Stamens inserted near the middle of the tube or below; anthers oblong, slightly longer than wide; filaments glabrous. Ovary with the placenta confined to the sutures, rarely with an extra row of ovules along the ovary wall between the sutures. Seeds smooth, round to slightly flattened. Probably tetraploids on the base number nine.

## KEY TO THE SERIES AND SPECIES

- a. Corolla orifice usually naked, without faucal fimbriae, or fimbriate and the calyx spathe-like.....Series I. ARCTOPHILAE
- b. Calyx split to the base along one side to form a membranaceous spathiform sheath, the lobes reduced to green, apical teeth. Southeastern Arizona, western Chihuahua and Durango, Mexico.....5. *G. wislizeni*
- bb. Calyx tubular, the lobes well developed; orifice of the corolla always naked, with no trace of fimbriae at the base of the lobes.
- c. Plants branched from the base or simple, the ascending basal branches frequently bearing reduced flowers.
- d. Corolla lobes 4; outer calyx lobes broad and foliaceous; ovary narrowly ovoid to ellipsoid; flowers in loose simple cymes or axillary and solitary, occasionally in aggregate cymes, rarely subtended by a pair of bract-like leaves. Alaska and Canada south to Montana.....6. *G. propinqua*
- dd. Corolla lobes 5; calyx lobes irregular but scarcely foliaceous; ovary generally broadly ovoid; flowers in compact terminal aggregate cymes or in a compact head due to reduction of the terminal internodes, subtended by the upper pair or pairs of bract-like leaves. Southwestern Greenland.....7. *G. aurea*
- cc. Plants generally branched above, the flowers of the branches about equal to those of the main stem, not reduced.
- e. Flowers perfect, about 2 cm. long; corolla lobes apiculate, half as long as the tube; calyx 4-10 mm. long. Maine to the southern Appalachians, westward to Minnesota, Missouri, and Arkansas.....8. *G. quinquefolia*
- ee. Flowers occasionally polygamous, about 1 cm. long; corolla lobes obtuse to rarely acute, one-third to half as long as the tube; calyx minute, about 2 mm. long. Southeastern Arizona to Coahuila, Mexico.....9. *G. microcalyx*
- aa. Orifice of the corolla with dense or scattered fimbriae at the base of the lobes.....Series II. AMARELLAE
- f. Corolla lobes as long as the tube; faucal fimbriae free, rather thick and blunt, somewhat hyaline; capsule with a few (6 or less) oblong seeds. Southwestern Utah to southwestern Nevada.....10. *G. tortuosa*
- ff. Corolla lobes shorter than the tube; faucal fimbriae slender, opaque; capsule with many ovoid seeds.
- g. Calyx tube shorter than or equal to the acute to obtuse lobes; faucal fimbriae free at the base (united in ssp. *heterosepala*); terminal flowers about equal in length to the lateral ones. Labrador and Newfoundland to Maine and Vermont; westward to Alaska and southward in the mountains to Baja California; Black Hills; Rocky Mountains southward to central Mexico.....11. *G. amarella*
- gg. Calyx tube longer than the rounded, frequently auriculate lobes; faucal fimbriae united at the base; terminal flowers larger than the lateral. Attu Island, Aleutian Islands, Alaska.....12. *G. auriculata*



## Series I. ARCTOPHILAE J. M. Gillett, ser. nov.

*Aloitis* Raf. Fl. Tellur. 3:21. 1837. (T.: *A. quinquefolia* (L.) Raf.)

*Gentiana* L. sect. *Arctophila* Griseb. Gen. et Sp. Gent. 250. 1839.

5. GENTIANELLA *wislizeni* (Engelm.) J. M. Gillett, comb. nov.

*Gentiana wislizeni* Engelm., in Trans. Acad. Sci. St. Louis 2:215. 1862. (T.: *Wislizenus* 206!)

*Amarella wislizeni* (Engelm.) Greene, Leaf. Bot. Obs. & Crit. 1:53. 1904.

Annuals 1–5 dm. tall; stems prominently angled, branched above the base, the branches ascending. Basal leaves ovate, oblanceolate, elliptic to spatulate, 5–20 mm. long, 3–6 mm. wide, soon withering and frequently deciduous, occasionally forming a loose rosette; median leaves ovate to lanceolate, the apices obtuse in leaves of the lower third of the plant, becoming acute above, the base cordate and clasping, 15–35 mm. long, 5–15 mm. wide; upper leaves similar to the median but becoming progressively more lanceolate, the tips acute. Flowers axillary or terminal, in aggregate cymes, rarely in simple cymes or solitary, the flowers frequently secund or nodding; pedicels straight or strongly curved particularly when young, 3–20 mm. long. Calyx 4–6 mm. long, slit to the base along one side to form a membranaceous spathiform sheath partially enclosing the corolla, the lobes reduced to 4–5 minute, green teeth borne on the rim of the sheath. Corolla pale blue or white, tubular to narrowly funnelform, 6–13 mm. long, 2–4 mm. wide at the orifice, the lobes triangular-ovate, acuminate, one-fourth the length of the tube, very widely spreading, bearing at the orifice few to many ciliate fimbriae, or naked, the interfilamental glands distinct and swollen, more or less oblong-scutiform. Stamens slightly exserted, the filaments inserted near the middle of the corolla tube, the wings about 2.5 mm. wide at the base and tapering slightly above; anthers oblong, 0.8–1.1 mm. long, about 0.75 mm. wide, versatile and attached near the middle. Pistil subsessile or with a gynophore not exceeding 1 mm. long, the ovary linear-lanceolate, 7–8 mm. long, 1.0–1.5 mm. wide, stigmas sessile, oblong, 0.6 mm. long, 0.4 mm. wide, erect. Capsule longer than the marcescent corolla, up to 14 mm. long, dehiscent in the upper one-sixth, the valves recurving at the tip. Seeds ovoid, 0.75 mm. long, 0.5 mm. wide, distinctly flattened, the surface smooth, minutely wrinkled under high magnification, light brown.

In the White Mountains of Apache County and in the Chiricahua Mountains of Cochise County, Arizona; throughout the Sierra Madres of Chihuahua, and extending into Durango at altitudes of 2100–2500 m., on cool slopes and in stony pine woods; flowering throughout September and fruiting from late September until mid-October.

## UNITED STATES:

ARIZONA: Apache Co.: White Mts., *Rothrock* 799 (GH, MO, US). Cochise Co.: Chiricahua National Mon., Barfoot Park, Chiricahua Mts., *Blumer s. n.* (GH, NY, US), 177 (US), *Eggleston* 10819 (GH, US); Rustler Park, *Jones* 28730 (MO).

## MEXICO:

CHIHUAHUA: Sierra Madre, between Rio Chico and Rio Caballo, *Barlow s. n.* (F, US); Santo Domingo between Concheno and Pinos Altos, *Hewitt* 78 (GH); Mesa west of Hop

Valley, Jones *s. n.* (US); Pringle 1329 (F, GH, MEXU, NY, US), 1662 (MO, NY); near Colonia Garcia, Townsend & Barber 322 (F, GH, MO, NY, US); Collector unknown (MO); Pennell 19097, 19136 (US); Majarachie, Knobloch 5614 (F); mountains of Llanos, Wislizenus 206 (GH, MO).

DURANGO: road between San Julián and Cerro Pierto, Nelson 4950 (US).

The distinctive spathiform calyx assures instant recognition of *G. wislizeni*. The fimbriate corona at the orifice of the corolla is extremely variable, ranging from a dense row of ciliate fimbriae extending entirely across the base of each lobe to completely lacking in a few specimens. The lack of correlation between geography and the occurrence of plants with naked corollas prohibits recognition of them as a distinct taxon. Even as the criterion for a sporadic form the feature fails, since both types of flowers have been found on the same plant. Engelmann placed this species in *Gentiana* sect. ARCTOPHILA, perhaps because of the lack of fimbriae in most specimens that he examined, although both fimbriate and naked specimens were apparently seen by him.

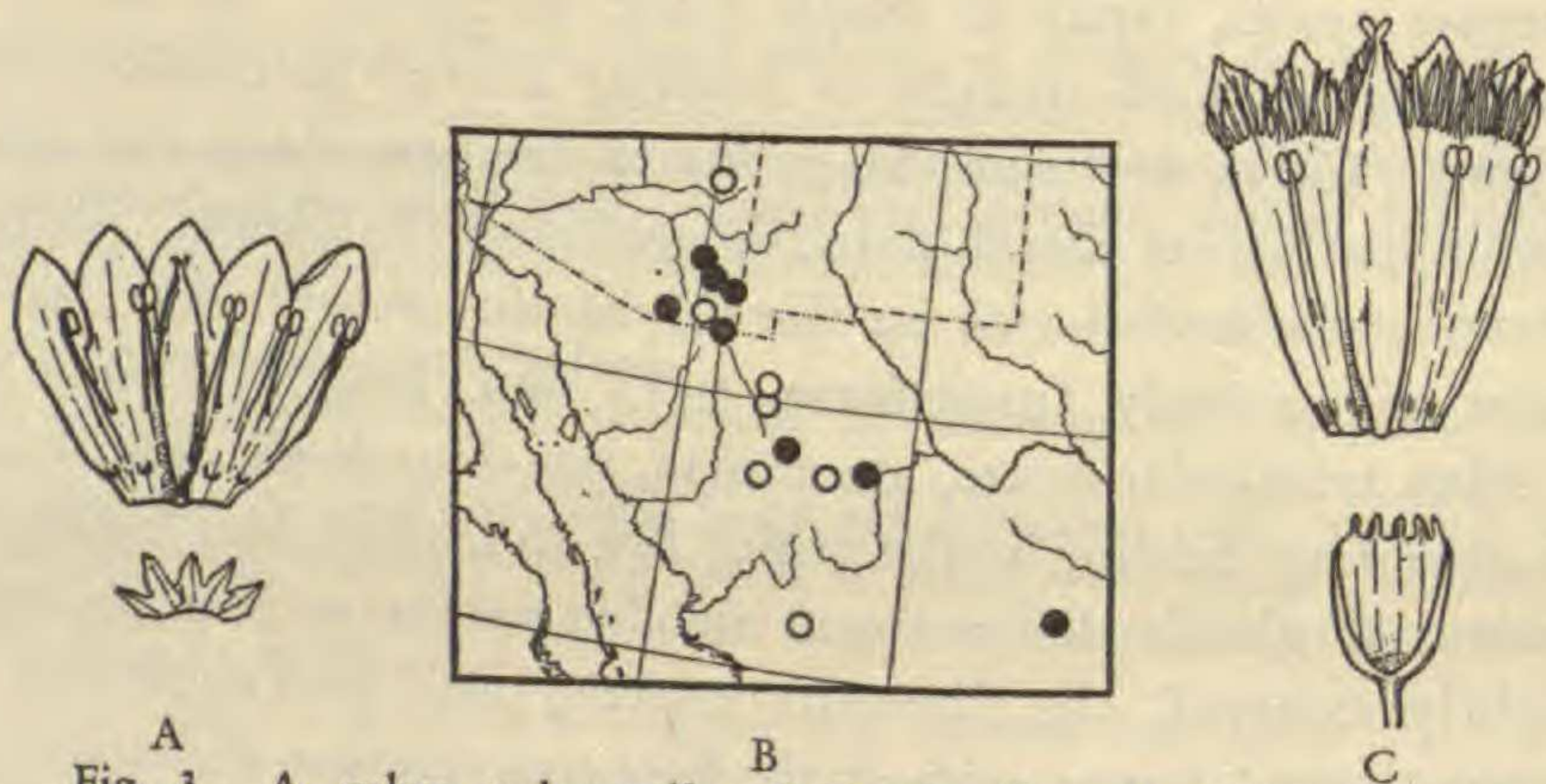


Fig. 3. A, calyx and corolla of *Gentianella microcalyx*,  $\times 1\frac{1}{2}$ . B, distribution of *G. wislizeni* (black dots) and of *G. microcalyx* (circles). C, calyx and corolla of *G. wislizeni*,  $\times 1\frac{1}{2}$ .

6. **GENTIANELLA propinqua** (Richards.) J. M. Gillett, comb. nov.

*Gentiana propinqua* Richards. in Frankl. Narr. 1st Jour. 734. 1823. (T.: Richardson *s. n.*, photo MO!)

Annuals 2–35 cm. tall, simple or branched from the base, the branches usually shorter than the main stem, curved-ascending, and bearing smaller flowers. Basal leaves frequently forming a dense rosette, elliptic to spatulate, the apex rounded to obtuse, gradually attenuate to the base, 5–35 mm. long, 2–8 mm. wide; median leaves ovate, ovate-elliptic to lanceolate, the apex acute to obtuse, the base generally broadened, rounded or clasping, 5–35 mm. long, 2–10 mm. wide; upper leaves similar to the median. Flowers 4-merous, axillary or terminal, in simple cymes or solitary, occasionally in aggregate cymes, the terminal flower conspicuously larger than the lateral ones or nearly equal in *ssp. aleutica*; pedicels 4–30 mm. long, the lateral flowers sessile or with pedicels correspondingly shorter. Calyx 5–12 mm. long, the tube 2–3 mm. long; lobes ovate to lanceolate, acute, the outer lobes wider than the inner, about twice as long as the tube, the margins minutely papillose-

toothed or entire, the sinuses acute. Corolla pale blue to white, tubular to narrowly funnelform, 12–20 mm. long, 3–5 mm. wide at the orifice, the lobes ovate to ovate-lanceolate, one-third to half the length of the tube, the tips mucronate or denticulate, the sinuses acute or more commonly concealed by the imbrication of the lobes, the orifice of the tube naked; interstaminal glands distinct, scutiform, and appearing as a pale green patch at or slightly above the base. Stamens included or slightly exerted, the filaments inserted about the middle of the corolla tube, the wings 0.25–0.50 mm. wide at the base and tapering slightly above; anthers oblong, 0.7–1.5 mm. long, 0.6–1.2 mm. wide, versatile and attached near the middle. Pistil very shortly stipitate, the gynophore 0.5 mm. long; ovary cylindrical, 7–10 mm. long, 1–2 mm. wide; stigmas sessile, elliptic, 1.25 mm. long, 0.4 mm. wide, erect. Capsule longer than the marcescent corolla, up to 25 mm. long, dehiscent in the upper fourth. Seeds ovoid, slightly flattened, 0.5–0.75 mm. long, 0.5–0.6 mm. wide, smooth, minutely wrinkled under magnification, light tan to dark brown.

Throughout Alaska and the Yukon on mountains and in valleys, extending through the Rockies to west-central Alberta and east-central British Columbia; from the Arctic Ocean occurring sporadically to the shores of Hudson Bay, with isolated stations in Beaverhead County, Montana, Gaspé County, Quebec, and the Straits of Belle Isle in Newfoundland; in a wide variety of habitats, such as alpine meadows, rocky shady hillsides, open sandy clay, gravel, or limestone areas, pine or mixed forests and in clearings, along streams and borders of marshes and in muskegs, on glacial moraines and on sea beaches, at altitudes from sea-level to about 3000 meters; flowering from mid-June until early September, fruiting from August until late September.

#### KEY TO THE SUBSPECIES

- a. Terminal flowers 15–20 mm. long, conspicuously larger than the lateral; corolla lobes apiculate, blue. Newfoundland to Alaska south to Montana.....6a. *G. propinqua* ssp. *propinqua*  
 aa. Terminal flowers about 10 mm. long, about as long as the lateral flowers or slightly larger; corolla lobes obtuse and somewhat denticulate, pale violet to white. Aleutian Islands to southern Alaska.....6b. *G. propinqua* ssp. *aleutica*

#### 6a. GENTIANELLA PROPINQUA (Richards.) ssp. PROPINQUA

- Gentiana rurikiana* Cham. & Schlecht. in *Linnaea* 1:176. 1826, ex char. (T.: Chamisso s. n.)  
*Gentiana gracilis* Cham. & Schlecht. loc. cit. 1826, nom. nud.  
*Gentiana setiflora* Bunge, in *Mem. Soc. Imp. Nat. Mosc.* 7 (Nouv. Mem. Soc. Nat. Mosc. 1):242. t. 9. fig. 4. 1829, ex char. et icon.  
*Gentiana propinqua*  $\beta$  *densiflora* Griseb. in *Hook. Fl. Bor. Am.* 2:62. 1838. (T.: Drummond s. n. photo MO!)  
*Gentiana arctophila* Griseb. in *Hook. loc. cit.* 61. 1838. (T.: Richardson s. n.!)  
*Gentiana arctophila*  $\beta$  *densiflora* Griseb. in *Hook. loc. cit.* 1838. (T.: Drummond s. n.!)  
*Amarella propinqua* (Richards.) Greene, *Leafl. Bot. Obs. & Crit.* 1:53. 1904.  
*Amarella arctophylla* (Griseb.) Greene, loc. cit. 1904.  
*Amarella ventorum* Rydb. in *Bull. Torr. Bot. Club* 40:463. 1913, ex char. (T.: Fremont s. n.?)

Newfoundland to Alaska and southward in the Rocky Mountains to western Montana.

## UNITED STATES:

ALASKA: Donnelly Dome, Mile 250, Richardson Highway, *Cody 6294* (DAO); Jarvis Creek, Mile 267, Richardson Hwy, *Cody & Webster 5957* (DAO); near Delta Junction, *Cody & Webster 6024* (DAO); Mile 36, Slana-Tok Hwy. *Anderson 8691* (CAN); Kobuk River, *Palmer 652* (F); Umiat, Colville River, *Spetzman 2100* (CAN); Ignek Valley, *Spetzman 1470* (CAN); Sadlerochit River, *Spetzman 1001* (CAN); White Mts., Sheep and Mascot creeks, *Gjaerevoll 389* (CAN); Bennett, *Cowles 994* (MO); Yukon River between Rampart and Tanana, *Palmer 17* (CAN); Kotzebue-Lund, *Eschscholtz s. n.* (MO); Nome, *Jones 9165* (MO); Eagle Summit, *Lepage 25381* (DAO); Savage River, *Mexia 2100* (DAO, MO); Mt. McKinley Nat. Park, Mile 66, *Nelson & Nelson 3978* (GH, MO, NY); Alaska Range, Nenana Valley, *Porsild & Porsild 367* (CAN, GH); Castner Glacier, *Porsild & Porsild 503* (CAN, GH); between Summit and McCarty, *Porsild & Porsild 439* (CAN, GH); Kokrines Hills above Yukon River, *Porsild & Porsild 681* (GH); Pastolik, Norton Sound, *Porsild & Porsild 1015* (CAN, GH); near Bluff, Seward Peninsula, *Porsild & Porsild 1269* (CAN, GH); Mile 189, Richardson Hwy., *Webster 121* (DAO); Fort Yukon, *Kennicott s. n.* (F).

MONTANA: Beaverhead Co.: Sheep Mountain, *Hitchcock & Mublick 12887* (MO, WS).

## CANADA:

ALBERTA: Lake Louise, *Anderson s. n.* (CAN, WS), *Lasalle 45105* (CAN); Pabatac Creek, *Brown 1342* (MO); Vermillion Slope, *Fletcher s. n.* (DAO); Blair Mt., *Lambert s. n.* (CAN); Banff National Park, Bow Peak, *Hitchcock & Martin 7741* (plants #2, 5 GH, WS); near Banff, *Macoun s. n.* (MO); Sunwapta Pass, *Ledingham 49-605* (DAO); Wicked River, near Peace River, *Raup & Abbe 4331* (CAN); Smoky River, *Riley 35* (US); Jasper National Park, Mt. Edith Cavell, *Ledingham 49-627* (DAO); Miette Hot Springs, *Turner 5134* (DAO); Athabasca Falls, *Turner 6948* (CAN, DAO); Peyto Glacier, *Weber 2440* (WS).

BRITISH COLUMBIA: Mt. Pope, n.w. Ft. St. James, *Calder, Savile & Ferguson 13798* (DAO); Mt. Thornhill, near Terrace, *Calder, Savile & Ferguson 14839* (DAO); Murray Range, Azousetta Lake, *Calder, Savile & Ferguson 14059* (DAO); Mt. McLean at Lillooet, *Calder, Savile & Ferguson 15517* (DAO); Yoho Mt., *Bostock s. n.* (DAO); Mt. Stephen near Field, *Calder & Savile 12038* (DAO); Field, Lake O'Hara, *Brown 951* (MO); between Field and Mt. Wapta, *Walcott s. n.* (US); Burgess Pass, *Fyles s. n.* (DAO); Marble Canyon, *Grob s. n.* (DAO); Kicking Horse Lake, *Macoun s. n.* (CAN, DAO, GH, US); Chilliwack Valley, *Macoun s. n.* (US); Bennett, *Cowles 994* (F); Chipuin Mt., Marble Mts., *Thompson & Thompson 558* (CAN, MO, NY, PH, US); Paradise Mine, Windermere, *Calder & Savile 11265* (DAO); Loggan, *Macoun s. n.* (F); Atlin Lake, *Aitken 21* (DAO); Tonquin Valley, Jasper Park, *Kindle s. n.* (CAN); N. Kootenay Pass, *Dawson s. n.* (CAN); Mt. Selwyn, *Raup & Abbe 4055* (CAN).

MACKENZIE DISTRICT: Coppermine, *Findlay 240* (DAO); Dismal Lake, *Hall s. n.* (UBC); Bernard Harbour, *Johansen 372* (CAN, GH); Mackenzie River, *Onion, Kennicott & Hardisty s. n.* (PH); Bear Lake, *Richardson s. n.* (K TYPE, GH); Thelon River, Hornby's Bend, *Tener 266* (CAN); Thelon Game Sanctuary, The Angle, *Clarke s. n.* (CAN); Camp Franklin, Great Bear River, *Lindsey 523* (CAN); Canol Road, Mt. Range, Bolstead Creek, *Wynne-Edwards 8363* (CAN); Mark River, Lone Mt. near the North Nahanni River, *Wynne-Edwards 8505* (CAN); Liard River betw. Nahanni Butte and Simpson, *Crickmay 99* (CAN); Great Bear Lake, Dease River Valley, *Porsild & Porsild 4878* (CAN); McTavish Arm, *Porsild & Porsild 5182* (CAN); Leith Point, *Porsild & Porsild 3588* (CAN); Great Bear River, jct. Big Stick River, *Porsild & Porsild 3270* (CAN); Eskimo Lake basin, Setidgi Lake, *Porsild & Porsild 3162* (CAN); Kugaruk, n. Anderson River, *Porsild & Porsild 3088* (CAN); Liverpool Bay, Nicholson Island, *Porsild & Porsild 2927* (CAN); Mackenzie River delta, Kittigazuit Island, *Porsild & Porsild 2390* (CAN); Campbell Lake, Point Separation, *Porsild & Porsild 1957* (CAN); Richardson Mts., *Porsild & Porsild 6847* (CAN); Mackenzie Bay, *Stringer s. n.* (CAN).

FRANKLIN DISTRICT: Banks Island, n. of Cape Lambton, *Porsild 17593* (CAN); Victoria Island, vic. Holman Is. Trading Post, *Porsild 17328* (CAN); Banks Island, Nelson Head, *Manning & Macpherson 112* (CAN).

MANITOBA: Churchill, *Gillett 2340* (DAO, MO), *Macoun s. n.* (CAN), *Polunin 40* (CAN), *Porsild 5494* (CAN); York Factory, *Bell s. n.* (CAN), *Scoggan 6052* (CAN).

NEWFOUNDLAND: Mistaken Cove, Straits of Belle Isle, *Fernald, Long et al. 26975* (F).

ONTARIO: Cap Henriette, *Dutilly & Lepage 31244* (DAO); Lake River, *Smith 86* (CAN); South Twin Island, *Johansen 274* (CAN).

QUEBEC: Gaspé Co.: Anse Pleureuse, *Victorin & Germain 49435* (DAO); James Bay: Cap Jones, *Dutilly, Lepage & Duman 32527* (DAO).

YUKON TERRITORY: Dawson, *Calder & Billard 3380* (DAO), *Eastwood 425* (F); 60-mile road, West Dawson to Alaskan border, *Calder & Billard 4418* (DAO); Mayo Lake, *Green 24* (DAO); Whitehorse, *Gillett 3463, 3470, 3660, 3813, 3834* (DAO); Keno Hill, *Gillett, Calder et al. 4338* (DAO); North Fork, Klondike River, *Cockfield 51* (CAN); Cassiar Mts. 20–30 miles e. Teslin Lake, *Poole s. n.* (DAO); Lake Laberge, *Gillett & Mitchell 3959* (DAO); Big Salmon, Lewes River, *Gillett & Mitchell 3971* (DAO); Stewart Landing, *Gillett & Mitchell 4084* (DAO); Independence Creek, Stewart River, *Gillett & Mitchell 4134* (DAO); Mt. Caribou, nr. Carcross, *Gillett & Mitchell 4568* (DAO); Rampart House, *Loan 681* (DAO); Coffee Creek, *Malte 44, 50* (CAN, GH); Reindeer Creek, Yukon River, *Barton s. n.* (UBC); Bear Creek, nr. Lake Desert d'Asch, *Müller s. n.* (MO); Snag, *Noel 43* (CAN, UBC); Mile 180, north of Fort Nelson, *Williams s. n.* (UBC); Mackintosh, Alaska Hwy., mile 1022, *Anderson & Brown 10053* (CAN); Moosehide Mt., *Campbell 51* (JBM); Frith River, *McEwan 194* (CAN); Canol Road, Mt. Sheldon, *Porsild & Breitung 11753* (CAN); Mile 132, Lower Lapie River Crossing, *Porsild & Breitung 9991* (CAN); Mile 95, Upper Rose River valley, *Porsild & Breitung 10403* (CAN); Mile 36–42, Misutlin River, *Porsild & Breitung 10849* (CAN); Herschell Island, *Johansen 559* (CAN); Franklin Expedition, *Richardson s. n.* (CAN).

LOCATION UNKNOWN: Arctic Sea Coast, *Richardson s. n.* (CAN, GH); Rocky Mts., *Drummond s. n.* (K, GH).

*Gentianella propinqua* ssp. *propinqua* is recognized easily by the larger terminal flowers, with apiculate corolla lobes. These features, coupled with the ascending basal branches, provide good field characters for distinguishing *G. propinqua* from *G. amarella* ssp. *acuta* where these species occur together.

This species has been examined in the field, particularly in the Yukon. The height of the plant varies considerably in the Whitehorse area, simple and branched plants growing side by side in habitats ranging from forests of *Pinus contorta* var. *latifolia* to open bare sandy places. Numerous dead plants from previous years were found in sheltered wet places, their condition clearly indicating their annual character. At Carcross, Yukon Territory, I had an opportunity to climb Mt. Caribou and to observe that the plants decrease in size with increase in altitude without any apparent break in the population continuity, except perhaps on rock slides where growth of plants in general was curtailed.

A journey by steamer along the Lewes and Stewart rivers revealed an almost continuous distribution between Whitehorse and Mayo Landing.

At Churchill, Manitoba, the species was not common and was restricted to gravelly roadsides and to the edge of the airport runways.

A few specimens from southern British Columbia and the solitary specimen from Montana have corolla lobes that are broadened above the sinus and bear no apicula at the tip (*arctophila* type). Except that they occur in this general region, there appears to be no definite boundary to the population. One sheet, *Calder & Savile 12038*, collected at an altitude of 7,700 feet on Mount Stephens near Field,

B. C., bears both apiculate and exapiculate plants. The sixteen plants on the DAO sheet are all quite small and were found on an open heath near talus slopes. The smallest plant is 3 cm. high and bears a flower fully 2 cm. long with obtuse exapiculate lobes; the largest plant is 6 cm. tall and has normal apiculate flowers indistinguishable from many other collections.

During the summer of 1954, J. A. Calder and D. B. O. Savile encountered a patch of pure white-flowered *G. propinqua* located not more than a few yards away from the blue-flowered form. Although white-flowered forms occur among most colored-flowered plants, these plants show a complete lack of the purple coloration normally present in *G. propinqua*. Probably this is an expression of a recessive character, but because a considerable colony had apparently become established within the blue-flowered population, I feel justified in providing it with a name.

GENTIANELLA PROPINQUA (Richards.) J. M. Gillett forma *acyanea* J. M. Gillett, form. nov.

Plantae viridulae non purpureo-tinctae; floribus in vivo albis in sicco ochroleucis.

CANADA:

BRITISH COLUMBIA: Steep slope at base of cliffs at 5,000 ft. near head of valley, Western Uranium Mine about 9 miles ne. of Skeena Crossing, Aug. 30, 1954, *Calder, Savile & Ferguson 1520A* (DAO, HOLOTYPE); rare in deep shade of spruce woods, acid habitat and in moss by spring in muskeg, Mile 250, Richardson Hwy. near base of Donnelly Dome, Aug. 2, 1951, *Cody 6294* (DAO).

The paucity of data available to me prohibits any correlation of the characters of *G. arctophila*, as given by Grisebach, with either geographic area or altitude. Until such data are available, it seems best to relegate this name to synonymy of *G. propinqua*. However, the following comments regarding the types of *G. arctophila* and *G. arctophila*  $\beta$  *densiflora* may be of interest, should the necessity arise to give the populations taxonomic recognition.

A sheet from the Gray Herbarium has four different collections, among which one is labeled "*Gentiana arctophila* m. B.N.A. nr. 17."; below this specimen, in another hand, appear the words "R. Mts. Hook." Above the label are three plants, one of which is separated from the others by a line and labelled "Arctic Sea-coast". In the New York Botanical Garden Herbarium, a Meisner Herbarium sheet is labeled "*Gentiana arctophila* Gr. America arctica" in the same handwriting as the name on the Gray sheet. On this same label in a different hand is the comment "Com. cl. Grisebach 28/4/65." These specimens compare very closely with the photographs of the type from Kew.

This evidence seems to indicate that the Gray sheet, at least, consists of isotypes of both *G. arctophila* and *G. arctophila*  $\beta$  *densiflora* and that they were collected as stated by Grisebach (Hook. Fl. Bor.-Amer. 2:62): "HAB. Arctic Sea-Coast. Dr. Richardson.  $\beta$  Rocky Mountains. Mr. Drummond."

6b. *GENTIANELLA PROPINQUA* (Richards.) J. M. Gillett, ssp. *aleutica* (Cham. & Schlecht.) J. M. Gillett, comb. & stat. nov.

*Gentiana aleutica* Cham. & Schlecht. in *Linnaea* 1:175. 1826, ex char. (T.: *Chamisso* & *Eschscholtz s. n.*)

*Gentiana unalaschcensis* Cham. & Schlecht. loc. cit. 1826, nom. nud.

Throughout the Aleutian Islands, extending to the mainland as far as Juneau; mountains at elevations of 100–500 meters, in stony and mossy places, dry gullies and in grassy patches in gravel; flowering and fruiting throughout August.

UNITED STATES:

ALASKA: Mt. Roberts, Juneau, *Anderson* 2139 (NY); Port Vita, Raspberry Island, Kodiak group, *Eyerdam* 5236 (DAO); Semisopochnoi Island, *Coats* 75 (US); Unimak Island, False Pass, *Eyerdam* 2023 (NY, US); Jim Fishe Ridge, Attu Island, *Hardy* 297 (MO); Attu Island, vicinity Massacre Bay, Lookout Hill, *Van Schaack* 919 (MO), 935 (MO, US); Kodiak Island, Olga Bay, *Looff* & *Looff* 543 (GH), 530 (UBC); valley near Cannery Station, *Looff* & *Looff* 1689 (MO, NY); Volcano Mt., *Looff* & *Looff* 1598 (CAN); Cold Bay, *Schofield* 238 (DAO).

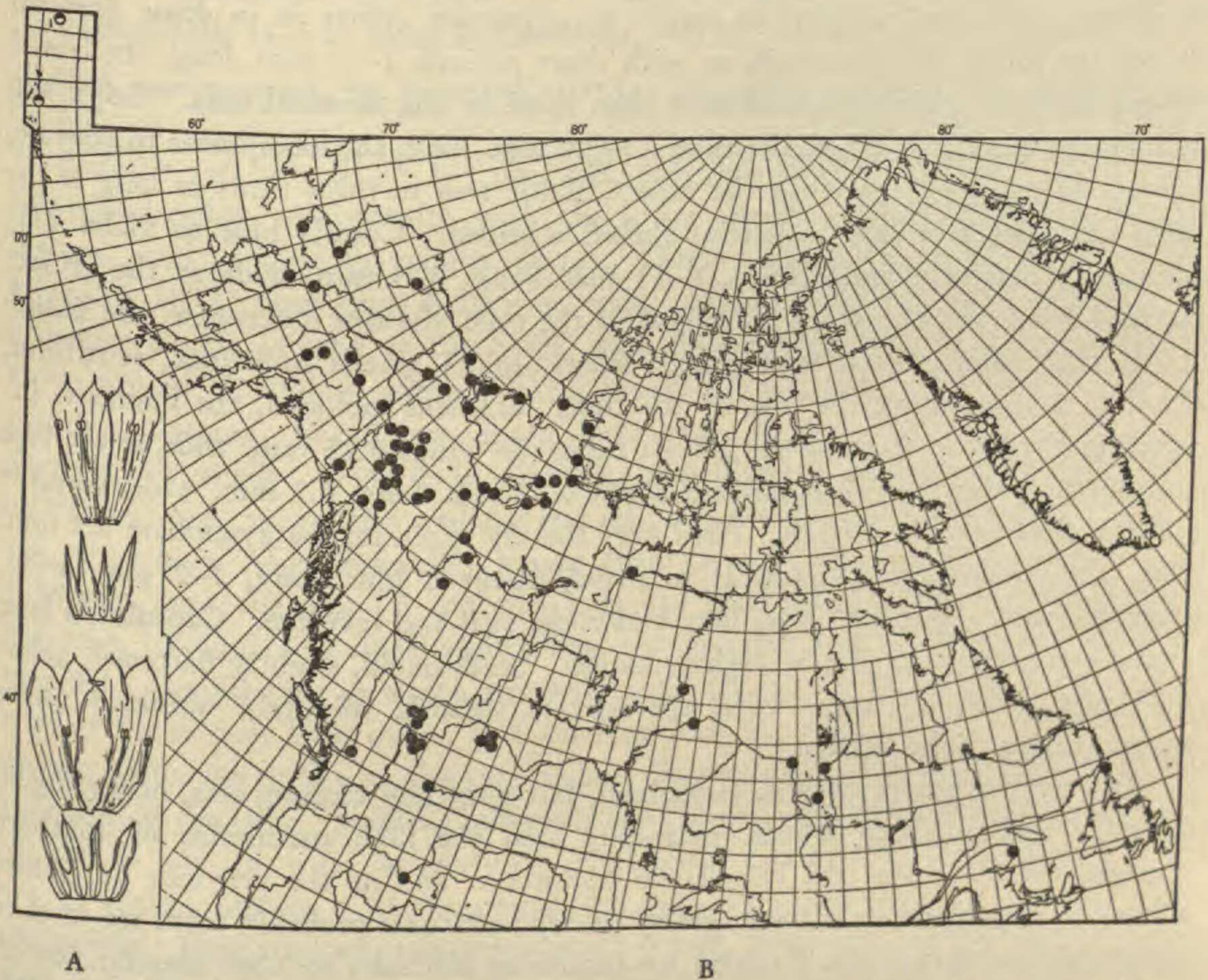


Fig. 4. A, calyx and corolla of *Gentianella propinqua* (above),  $\times \frac{3}{4}$ ; and of *G. aurea* (below),  $\times 1\frac{1}{2}$ . B, distribution of *G. propinqua* ssp. *propinqua* (black dots), of *G. propinqua* ssp. *aleutica* (half-black dots), and of *G. aurea* (circles).

7. *GENTIANELLA AUREA* (L.) H. Sm. ex Hylander, in Uppsala Univ. Arssk. 259. 1945.

*Gentiana aurea* L. Syst. ed. 10. 951, 1759. (T.: *Konig s. n.*, photo A!)

*Gentiana quinquefolia* Oeder, Fl. Dan. t. 344. 1766, not L., ex ic.

*Gentiana involucrata* Rottb. in Kiob. Skr. Selsk. 10:434. 1770. (T.: *Collector unknown*, C!)

*Gentiana umbellata* Marsch. & Bieb. Fl. Taur. Cauc. 3:188. 1819, ex char.

*Gentiana aurea a borealis a. genuina* Herder, in Acta Hort. Petrop. 1:438. 1872. (based on *G. aurea* L.)

*Gentiana Pseud-Amarella* Stev. ex Herder, loc. cit. 437. 1872, nom nud. in syn.

Annuals 2–30 cm. tall, simple or branched from the base, the branches curved-ascending, frequently bearing reduced flowers. Basal leaves frequently forming a rosette, elliptic to spatulate, the apex rounded to obtuse, attenuate to the base or to a slender petiole one-third the length of the blade, 3–21 mm. long, 1–10 mm. wide; median leaves lanceolate to ovate, the apex obtuse, the base rounded, 9–26 mm. long, 4–13 mm. wide; upper leaves similar and enclosing the terminal inflorescence. Flowers axillary, in simple or aggregate cymes or in dense terminal clusters, or rarely solitary, sessile or with short pedicels 1–13 mm. long, the lateral flowers sessile or with pedicels shorter than those of the terminal ones. Calyx 3–8 mm. long, generally 5-lobed, the tube 1.5–2.0 mm. long, the lobes linear to obovate, acute, two usually larger than the others, about two to three times as long as the tube, the margins ciliate to entire; sinuses rounded. Corolla blue to violet (?), tubular to narrowly funnelform, 6–11 mm. long, 3–5 mm. wide at the orifice; corolla lobes ovate, one-third the length of the tube, the tips mucronate, the sinuses acute, the orifice of the tube naked; interstaminal glands indistinct, scutiform, about 0.25 mm. above the base of the tube. Stamens included, the filaments inserted in the lower third of the corolla tube, the wings 0.25 mm. wide at the base and tapering above; anthers oblong, about 0.75 mm. long, 0.5 mm. wide, versatile and attached near the middle. Pistil very shortly stipitate, the gynophore 0.5 mm. long, the ovary short-cylindrical to ovoid, about 6 mm. long, 1–2 mm. wide; stigmas sessile, about 0.25 mm. long and wide, oval and revolute. Capsules as long as the marcescent corollas or slightly longer. Seeds ovoid, slightly flattened, about 0.75 mm. long, 0.6 mm. wide, the surface smooth, minutely wrinkled under magnification, light brown.

In North America only in Greenland, but generally circumpolar, occurring in Norway and northern Russia, extending into the high mountains of southern Europe, the Caucasus, the Himalayan Mountains and in the province of Kansu, China; in Greenland growing in grassy fields at altitudes probably from sea-level to about 300 meters; in the Eurasian mountains at altitudes to 3200 meters; flowering from mid-July until mid-August; fruiting until early September (Greenland).

GREENLAND: Igdlungujak, *Jessen s. n.* (C); Tigsaluk, ca. 61° 21', *Hartz s. n.* (C); Kingua, *Tasersuak, Hartz s. n.* (C); Tasermint, *Hartz s. n.* (C, GH, MO); Igaliko, *Hartz s. n.* (C); Kakasuak near Kringorsuak, *Kruuse s. n.* (C); Ekaluit i Igalikofjord, *Lindemann s. n.* (C); Frederiksdal, *Lundholm s. n.* (C); Igaliko, *Meldorf s. n.* (C); Kagsiarsuk, Tunugdliarfik Fjord, *Petersen in 1880* (C); Tunugdliarfik Fjord, Qagsiarsuk, 61° 10' N, 95° 30' W., *Porsild 8897* (CAN); Kagsiarsuk, Igalikofjord, *Rosenvinge in 1888* (CAN);



Igaliko (Gardar), 60° 59' N., *Porsild & Porsild s. n.* (C, GH); Igdlorssuit, Prins Christians Sund, 60° 10' N., *Porsild & Porsild* (C); Igaliko, *Rosenvinge s. n.* (C); Kingua i Tunugdliarfik, *Rosenvinge s. n.* (C); Isarok v. Semdlik, *Rosenvinge s. n.* (C); Igaliko, *Sorenson s. n.* (C); Kakortok, *Vahl s. n.* (C); Igaliko, Dist. Julianehaab, *Vahl s. n.* (C).

*Gentianella aurea* is easily distinguished by the dense, terminal flower clusters subtended by the ovate upper leaves. Because of the characteristic curved-ascending basal branching pattern, *G. aurea* somewhat resembles *G. propinqua*. Although some depauperate specimens lack this feature, the mucronate corolla tips are a good supplementary character for recognition.

Very little material has been seen from Greenland, and therefore European specimens have been employed in drawing up the description, for the latter appear to be similar to the Greenland plants in every respect. Very little habitat data are given with the Greenland plants, so that this information also is drawn chiefly from the European collections.

8. GENTIANELLA QUINQUEFOLIA (L.) Small, Fl. Southeast. U. S. 929. 1903. (*G. quinquefolia* (L.) D. Löve in *Hereditas* 39:227. 1953, superfluous comb.).

*Gentiana quinquefolia* L. Sp. Pl. 1:230. 1753. (T.: *Kalm s. n.*, Sav. Cat. 328.31, photo A!)

Annuals (or biennials?) 2–8 dm. tall, profusely branched above, the branches curved-ascending, occasionally with the lower slender branches bearing reduced flowers, rarely simple in smaller plants. Basal leaves elliptic-spatulate to sub-orbicular, 10–22 mm. long, 4–10 mm. wide, the apex rounded, attenuate below to a slender petiole as long as the blade, soon withering and both basal and lower leaves usually deciduous; median leaves broadly ovate, acute, the base cordate to rounded, clasping, 15–60 mm. long, 5–35 mm. wide; upper leaves similar but progressively smaller. Flowers in compact, umbelliform, aggregate cymes, terminal on the branches, very rarely axillary and solitary; pedicels 2–17 mm. long, those of the subterminal node frequently longer than those of the terminal node. Calyx 4–10 mm. long, the tube 1.5–3.5 mm. long, the lobes about equal to or longer than the tube, triangular to elliptic-lanceolate, the margins entire, the sinuses acute to rounded. Corolla blue to white, narrowly funnelform, 15–20 mm. long, 4–7 mm. wide at the orifice; lobes ovate, half the length of the tube, the tips apiculate, the sinuses acute, the orifice of the tube naked; interstaminal glands scutiform, at the very base of the tube. Stamens included, the filaments inserted about the middle of the corolla tube, the wings strongly incurved, about 1 mm. wide at the base, tapering above; anthers oblong, 1.75 mm. long, 0.5 mm. wide, versatile and attached near the middle. Pistil stipitate, the gynophore 2–3 mm. long; ovary cylindrical, 12 mm. long, 1.5 mm. wide; stigmas sessile, or with an indistinct style tapering into the ovary, oblong, 1 mm. long, 0.25 mm. wide, recurving. Capsule as long as the marcescent corolla, dehiscent at the tip. Seeds rounded or slightly flattened, 0.5–0.6 mm. long, the surface smooth, light brown.

A polymorphic species with two clearly distinct allopatric subspecies distinguished chiefly by flower and calyx size.

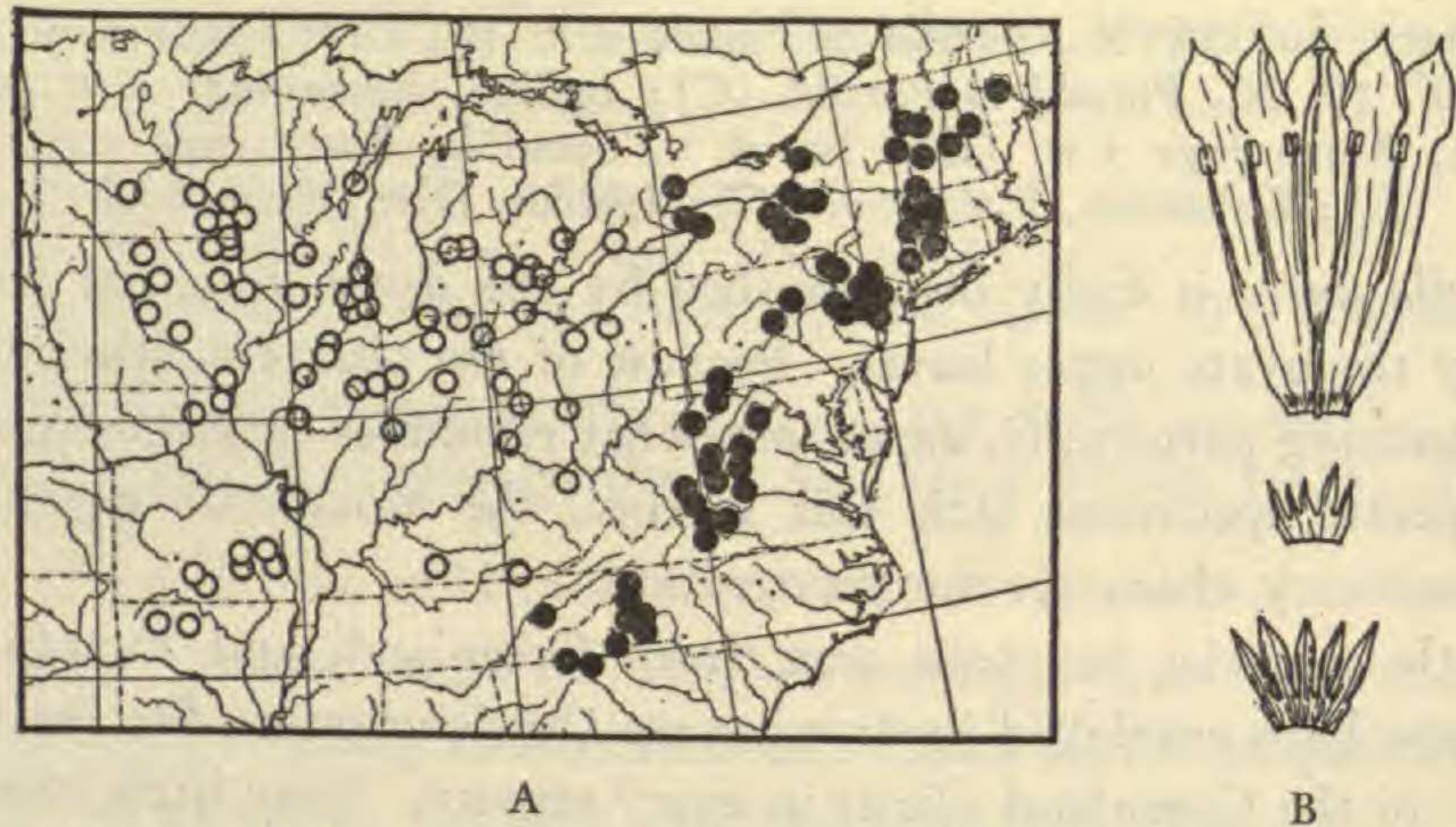


Fig. 5. A, distribution of *Gentianella quinquefolia* ssp. *quinquefolia* (black dots) and of ssp. *occidentalis* (circles). B, corolla of *G. quinquefolia* (top), calyx of ssp. *quinquefolia* (middle), and of ssp. *occidentalis* (bottom),  $\times 1\frac{1}{2}$ .

#### KEY TO THE SUBSPECIES

- a. Calyx 4–5 mm. long, the tube 1.5–2.0 mm. long, the lobes 2.0–2.5 mm. long, narrowly triangular with hyaline margins and very prominent keels; corolla 16–18 mm. long. Maine westward to New York and southern Ontario, southward to Georgia.....8a. *G. quinquefolia* ssp. *quinquefolia*
- aa. Calyx 8–10 mm. long, the tube 3.0–3.5 mm. long, the lobes 5–6 mm. long, elliptic-lanceolate to oblanceolate with thickened margins and broadly flattened, frequently nerve-like, keels; corolla about 20 mm. long. Ohio to Minnesota, southward to Arkansas and Kentucky.....8b. *G. quinquefolia* ssp. *occidentalis*

#### 8a. GENTIANELLA QUINQUEFOLIA (L.) Small, ssp. QUINQUEFOLIA

*Gentiana quinqueflora* Lam. Encyc. 2. 643. 1768, sphalm?

*Hippion quinquefolium* (L.) Schmidt, in Roem. Archiv f. Bot. 1:11. 1796.

*Gentiana amarelloides* Michx. Fl. Bor. Am. 1:175. 1805. (T.: Michaux s. n., photo MO!)

*Aloitis parviflora* Raf. Fl. Tellur. 3:21. 1837, ex char.

*Aloitis quinqueflora* (L. emend. Lam.) Raf. loc. cit. 22. 1837.

*Gentiana quinqueflora* Lam.  $\beta$  *parviflora* Raf. ex Griseb. in DC. Prod. 9:100. 1845, ex char.

*Gentiana quinquefolia* L. var. *amarelloides* (Michx.) Britt. in Mem. Torr. Bot. Club 5:260. 1894.

*Aloitis divaricata* Greene, Leaf. Bot. Obs. & Crit. 1:94. 1904.

*Amarella amarelloides* (Michx.) Greene, loc. cit. 53. 1904.

*Gentiana quinquefolia* L. f. *lutescens* Fern. in Rhodora 19:151. 1917. (T.: Porter s. n.!)

Maine to New York and southern Ontario southward in the Appalachians to North Carolina and Tennessee, at altitudes up to 1800 meters in the southern Appalachians; in a variety of habitats, but chiefly on edges of woods in shady places, roadsides, and along stream banks; apparently preferring limestone areas or lime soils; flowering from early September until early October, rarely until November; fruiting during the latter part of October.

#### CANADA:

ONTARIO: Elgin Co.: Fisher s. n. (MO). Lambton Co.: Forest, Dodge s. n. (MO). Welland Co.: Niagara Falls, Scott s. n. (US). York Co.: Toronto, Armstrong s. n. (US).

## UNITED STATES:

- CONNECTICUT: Litchfield Co.: South Canaan, *Greenman 1444* (GH, MO).  
 GEORGIA: Rabun Co.: Blalock, *Wherry & Pennell 14087* (F, MO).  
 MAINE: Oxford Co.: Norway, *Olmstead s. n.* (GH).  
 MARYLAND: Garrett Co.: Oakland, *Hermann 11380* (MO).  
 MASSACHUSETTS: Berkshire Co.: Kitchen Brook, *Churchill s. n.* (GH, MO).  
 NEW HAMPSHIRE: Grafton Co.: Squam Lake, *Faxon s. n.* (GH, US).  
 NEW JERSEY: Sussex Co.: High Point, *Mackenzie 4408* (MO). Warren Co.: Phillipsburg, *Garber s. n.* (WS).  
 NEW YORK: Cayuga Co.: *Hall s. n.* (MO). Columbia Co.: Columbiaville, *McVaugh 4037* (GH). Dutchess Co.: Clove, *Standley & Bollman 12361* (US). Erie Co.: *Clinton s. n.* (NY). Jefferson Co.: Watertown, *Keyes s. n.* (US). Madison Co.: Chittenango, *Morong s. n.* (US). Onondaga Co.: Syracuse, *Overacker s. n.* (MO). Orange Co.: Brookfield, *Collector unknown* (MO). Oswego Co.: Phoenix, *Hastings s. n.* (NY). Schuyler Co.: Hector, *Wright 10612* (GH). Seneca Co.: West Junius, *Schrenk s. n.* (MO). Tompkins Co.: Ithaca, *Sheldon s. n.* (US). Warren Co.: Lake George, *House 25991* (MO). Washington Co.: Tripoli, *Burnham s. n.* (GH).  
 NORTH CAROLINA: Buncombe Co.: Biltmore, *Biltmore Herb. 465b* (GH, MO, US). Haywood Co.: Pisgah Forest, *House 3696* (GH). McDowell Co.: Little Roan, *Merriam s. n.* (GH, MO, NY, US). Polk Co.: Columbus, *Townsend s. n.* (US). Yancey Co.: Busick, *Wherry & Pennell 14279* (MO).  
 PENNSYLVANIA: Center Co.: Coburn, *Whyt 271* (GH). Chester Co.: *Porter s. n.* (GH). Lackawanna Co.: Carbondale, *Topping s. n.* (US). Luzerne Co.: Long Pond, *Small & Heller s. n.* (US). Lycoming Co.: Williamsport, *Smith s. n.* (PH). Monroe Co.: Naomi Pines, *Small s. n.* (US). Northhampton Co.: Easton, *Heller 630* (MO, US). Somerset Co.: *Rotbrock s. n.* (F).  
 TENNESSEE: Carter Co.: Roan Mountain, *Britton & Britton s. n.* (NY).  
 VERMONT: Addison Co.: Weybridge, *Brainerd s. n.* (NY). Bennington Co.: Manchester, *Day 405* (US). Caledonia Co.: East Barnett, *Blanchard s. n.* (GH). Orange Co.: Strafford, *Jones s. n.* (GH); Rutland, *Eggleston 1503* (US).  
 VIRGINIA: Augusta Co.: Augusta Springs, *Steele s. n.* (MO, US). Bedford Co.: Peaks of Otter, *Beyrich 87* (MO, NY). Botetourt Co.: Apple Orchard Mountain, *Freer 1902* (GH). Frederick Co.: Cedar Creek, *Canby s. n.* (US). Highland Co.: Shenandoah Mt., *Rawlinson 272* (US). Madison Co.: Shenandoah Nat. Park, *Graf 3* (US). Nelson Co.: Afton, *Steele s. n.* (US). Page Co.: Hawksbill Mt., *Baldwin 5461* (GH). Roanoke Co.: Singer, *Wood 5701* (GH). Rockbridge Co.: *Steele s. n.* (US).  
 WEST VIRGINIA: Greenbrier Co.: Kate's Mt., *Hunnewell 7105* (GH). Monroe and Allegheny Cos.: Allegheny Station, *Steele & Steele 418* (GH, MO, US). Pendleton Co.: Lake Terra Alta, *Berkley 1781* (MO). Preston Co.: Brookside, *Olds s. n.* (US).

8b. GENTIANELLA QUINQUEFOLIA (L.) Small, ssp. *occidentalis* (A. Gray)

J. M. Gillett, comb. &amp; stat. nov.

- Gentiana quinqueflora* Lam. var. *occidentalis* A. Gray, Man. ed. 1, 359. 1848, based on Hook. Bot. Mag. 63: t. 3496. 1836. (c.f. Gray in Syn. Fl. N. Amer. 2:119. 1878).  
*Gentiana quinquefolia* L. var. *occidentalis* (A. Gray) A. S. Hitchc. in Trans. Acad. Sci. St. Louis 5:508. 1891.  
*Gentianella quinquefolia* (L.) Small, var. *occidentalis* (A. Gray) Small, Fl. Southeast. U.S. 929. 1903.  
*Amarella occidentalis* (A. Gray) Greene, Leaf. Bot. Obs. & Crit. 1:53. 1904.  
*Aloitis mesochora* Greene, loc. cit. 94. 1904, ex char.  
*Aloitis occidentalis* (A. Gray) Greene, loc. cit. 1904.  
*Aloitis foliosa* Greene, loc. cit. 1904. (T.: *Moseley s. n.*!)  
*Gentiana occidentalis* (A. Gray) Fitzpat. in Iowa Nat. 2:13. 1906.

Ohio westward to Wisconsin, Iowa and Minnesota, south to Arkansas and Kentucky; occurring in much the same habitats as the typical subspecies but also found on prairies and along wooded oak-juniper bluffs and wooded hillsides; as in the

typical subspecies, seeming to prefer limestone areas and wet stream gullies; flowering dates similar to the typical subspecies.

UNITED STATES:

ARKANSAS: Newton Co.: Vendor, *Iltis s. n.* (U. Ark.). Stone Co.: Blanchard Springs, *Iltis s. n.* (U. Ark.).

ILLINOIS: Champaign Co.: Rantoul, *Gleason s. n.* (GH). Cook Co.: Glencoe, *Umbach s. n.* (GH, PH). Hancock Co.: Augusta, *Mead s. n.* (MO). Lake Co.: Lake Forest, *Jensen 113* (MO). Kane Co.: Aurora, *Kane s. n.* (PH, US). LaSalle Co.: Ottawa, *Huett s. n.* (GH). Menard Co.: Athens, *Hall s. n.* (MO, PH, US). Peoria Co.: Peoria, *McDonald s. n.* (GH, NY). St. Clair Co.: French Village, *Eggert s. n.* (GH, MO). Stephenson Co.: Freeport, *Johnson s. n.* (US). Tazewell Co.: East Peoria, *Chase 3724* (US). Vermilion Co.: Fithian, *Gates 2175* (US).

INDIANA: Allen Co.: St. Joe River, Robinson Park, *Deam 606* (MO, NY, US). Benton Co.: *Shipman s. n.* (PH). Howard Co.: Wildcat, *Collector unknown* (NY). Lagrange Co.: Mongo, *Deam 19264* (GH). Marshall Co.: Lake Maxinkuckee, *Scovell & Clark 1459* (US). St. Joseph Co.: Notre Dame, *Nieuwland 10406* (US). Vigo Co.: Terre Haute, *Evermann s. n.* (US).

IOWA: Allamakee Co.: Hanover Twp., *Tolstead s. n.* (MO). Cerro Gordo Co.: Mason City, *Shimek s. n.* (WS). Dubuque Co.: Luxemburg, *Shimek s. n.* (MO). Fayette Co.: *Fink 487* (GH, US). Hamilton Co.: Webster City, *Hayden 10221* (GH). Hardin Co.: Iowa Falls, *Peck s. n.* (GH). Poweshiek Co.: Grinnell, *Jones s. n.* (GH). Story Co.: Ames, *Bessey 301* (GH, MO, US). Van Buren Co.: Bentonsport, *Graves s. n.* (MO). Winneshiek Co.: Ridgeway, *Hayden 10222* (US).

KENTUCKY: *Short s. n.* (MO, PH).

MICHIGAN: Genesee Co.: Flint, *Clark 5* (US). Ingham Co.: Lansing, *Tracy s. n.* (US). Ionia Co.: Hubbardston, *Wheeler s. n.* (US). Kent Co.: Grand Rapids, *Cole s. n.* (MO). Saint Clair Co.: Port Huron, *Dodge s. n.* (GH, MO). Washtenaw Co.: Dexter, *Palmer s. n.* (US). Wayne Co.: Woodbridge Park, *Chandler s. n.* (US).

MINNESOTA: Houston Co.: *Freiberg s. n.* (MO). Nicollet Co.: St. Peters, *Geyer 234* (MO). Olmstead Co.: Pleasant Grove Twp., *Moore, Leedy & Thatcher 15689* (DAO). Wabasha Co.: Lake City, *Manning s. n.* (GH). Winona Co.: Whitman, *Moore & Neva 16152* (MO, WS).

MISSOURI: Adair Co.: *Broadhead s. n.* (MO). Carter Co.: Van Buren, *Palmer 19450* (MO). Clark Co.: *Bush s. n.* (MO, NY). Douglas Co.: Hebron, *Steyermark 65102* (F). Howell Co.: 5 mi. s.w. Willow Springs, *Steyermark 66795* (DAO, F). Franklin Co.: Pacific, *Eggert s. n.* (MO). Iron Co.: Royal Gorge, *Kellogg 15260* (MO). Madison Co.: Jewett, *Steyermark 20985* (MO). Reynolds Co.: Lesterville, *Steyermark 20885* (MO). Shannon Co.: Monteer, *Steyermark 8771* (MO).

OHIO: Cuhahoga Co.: *Cook s. n.* (GH). Erie Co.: East Fork, Vermilion River, *Moseley s. n.* (F, MO, US). Franklin Co.: Georgeville, *Werner 539* (GH). Hamilton Co.: *Collector unknown* (PH). Lucas Co.: Monclova, *Moseley s. n.* (F, US). Mercer Co.: *Collector unknown* (PH). Montgomery Co.: Dayton, *Short s. n.* (PH).

WISCONSIN: Brown Co.: Scott, *Schuetz s. n.* (GH). Buffalo Co.: Fountain City, *Palmer 28496* (MO). Dane Co.: Madison, *McMurphy s. n.* (US). Lacrosse Co.: *Pammel s. n.* (MO). Racine and Kenosha Cos.: *Wadmond s. n.* (PH). Vernon Co.: Coon Valley, *Marks 1988* (DAO).

9. *GENTIANELLA microcalyx* (Lemmon) J. M. Gillett, comb. nov.

*Gentiana microcalyx* Lemmon in Pacific Rural Press 23:129. Feb. 25, 1882; Engelm. ex A. Gray, in Proc. Amer. Acad. 17:222. 1882. (T.: Lemmon 584!)  
*Amarella microcalyx* (Lemmon) Greene, Leaf. Bot. Obs. & Crit. 1:53. 1904.

Annuals 15–45 cm. tall; stems prominently angled, generally branched above, rarely from the base, the branches sharply ascending. Basal leaves oblanceolate, elliptic, to spatulate, the apex rounded to obtuse, attenuate to the base, 10–25 mm.

long, 2–8 mm. wide, soon withering and deciduous; median leaves broadly ovate to lanceolate-ovate, the apex acute, cordate or rounded and clasping at the base, 5–40 mm. long, 3–20 mm. wide; upper leaves similar to the median, becoming progressively more lanceolate. Flowers perfect, occasionally unisexual by abortion of the anthers (or, more rarely, the pistil), in compact umbelliform aggregate cymes, terminal on the branches, very rarely axillary and solitary; pedicels of the terminal flowers about equal, 3–15 mm. long. Calyx minute, 2.0–2.5 mm. long, 4- to 5-lobed, the tube 1 mm. long; lobes triangular, acute, essentially regular, about equal to the length of the tube or slightly longer, the margins entire, the sinuses rounded. Corolla white to pale lavender, tubular, narrowly funnelform or salverform when the lobes are fully expanded, about 10 mm. long, 2–3 mm. wide at the orifice; lobes oblong, one-third to half as long as the tube, the tips obtuse to rounded, the sinuses acute, the orifice of the tube naked; interstaminal glands indistinct, appearing only as dark oblong stains by transmitted light, 0.5 mm. from the base of the tube. Stamens slightly exerted; filaments inserted near the upper third of the corolla tube, scarcely winged, the wings about 0.25 mm. wide at the base, tapering above; anthers oblong, 1.3 mm. long, 0.8 mm. wide, versatile and attached near the middle. Pistil shortly stipitate, the gynophore 0.5 mm. long, ovary cylindrical, 11 mm. long, about 2 mm. wide; stigmas sessile, oblong, 0.4 mm. long, 0.2 mm. wide, erect. Mature capsule longer than the marcescent corolla, 12 mm. long, dehiscent at the tip. Seeds ovoid, slightly flattened, 0.75 mm. long, 0.5 mm. wide, smooth, light brown.

In the Huachuca Mountains of Cochise County, the Rincon and Santa Catalina mountains of Pima County, and in the Santa Rita Mountains of both Pima and Santa Cruz counties, Arizona; in Mexico in the Sierra Madres of southwestern and central Chihuahua, eastern Sonora, eastwards in the mountains about Cuatro Cienegas, Coahuila, southward to Durango; in cool moist pine-oak forest and on burnt-over slopes at altitudes of 600–2000 meters; flowering from late August until the end of September; fruiting in October.

UNITED STATES:

ARIZONA: Cochise Co.: Huachuca Mts., Carr Peak, *Goodding 858* (GH, NY); Carr Canyon, *Gould & Haskell 3373* (GH, MO), *Jones s. n.* (GH); Ramsey Canyon, *Jones 24967* (GH, MO, NY), *Lemmon 584* (GH, MO, US); Cave Canyon, *Lemmon 2822* (F, GH, US), *Peebles, Harrison et al. 3399* (US); Fort Huachuca, *Wilcox 507* (US); Towner's Canyon, *Wilcox s. n.* (NY). Pima Co.: Rincon Mts., Manning Camp, *Blumer s. n.* (F, GH, MO); Santa Rita Mts., *Griffiths 6049* (US), *Griffiths & Thornber 182* (US), *Loomis 3269* (US); Santa Catalina Mts., Mt. Lemmon, *Harrison 3020* (US), *Heally 191* (US); Marshall Gulch, *Shreve 5394* (GH, UC, US). Santa Cruz Co.: Santa Rita Mts., Kent Canyon, *Pilsbry s. n.* (PH), *Wootton s. n.* (US); location unknown, *Toumey s. n.* (US).

MEXICO:

CHIHUAHUA: Temosachic, Madera, *Muller 3465* (GH).  
 COAHUILA: Cuatro Cienegas, Sierra de la Madera, *Muller 3235* (MO).  
 DURANGO: Barranca Sandia Station, *Pringle 13660* (GH).  
 SONORA: Rio de Bavispe, 4 mi. e. El Belito, *White 4771* (GH).

## Series II. AMARELLAE J. M. Gillett, ser. nov.

*Amarella* Gilib. Fl. Lith. Inch. 1:36. 1781, nom nud.; Raf. Fl. Tellur. 3:20. 1837. (T.: *Anthopogon amarella* (L.) Raf.)

*Gentiana* L. \**Coelanthae* Froel. Gent. Diss. 15. 1796, proparte.

*Gentiana* L. \*\*\**Endotrichae* Froel. loc. cit. 86. 1796, ut sectio Murbeck, in Acta Hort. Berg. 23:1-28. 1892.

*Eyrythalia* Borckh. in Roem. Archiv f. Bot. 1:28. 1796, pro parte maj.

*Gentiana* L. \*\**Amarella* Gaudin, Fl. Helv. 2:270. 1828; ut sectio Griseb. Gen. et Sp. Gent. 238. 1839.

10. *GENTIANELLA tortuosa* (M. E. Jones) J. M. Gillett, comb. nov.

*Gentiana tortuosa* M. E. Jones, in Proc. Calif. Acad. II, 5:707. 1895. (T.: M. E. Jones 6008!)

*Amarella tortuosa* (M. E. Jones) Rydb. in Bull. Torr. Bot. Club 40:463. 1913.

*Gentiana helleri* Briq. in Candollea 4:331. 1931. (T.: Heller 11072!)

Acaulescent or caulescent, cespitose annuals 2-8 cm. tall, from very long tap-roots. Basal leaves elliptic, lingulate, to spatulate, the apex rounded or obtuse, attenuate below to about the width of the stem, clasping, 5-25 mm. long, 2-6 mm. wide; median leaves elliptic, oblong, or lanceolate, obtuse to acute, the base attenuate, 5-35 mm. long, 1-5 mm. wide. Flowers solitary in the axils of the stem leaves, or on short axillary branches; pedicels short to 15 mm. long. Calyx 5-7 mm. long, the tube very short, 1-2 mm. long, the lobes closely enclosing the corolla tube, linear to oblanceolate, acute, unequal, the margin hyaline and papillose, the sinuses rounded. Corolla white (or pale blue?), broadly funnelform to somewhat campanulate, 5-8 mm. long, 3-4 mm. wide; lobes ovate, obtuse, equaling the length of the tube, bearing a corona of 2-10 hyaline, papillose-margined fimbriae one-third the length of the lobes and extending across the base or in two distinct clusters on each side, the lower flowers occasionally naked, the sinuses acute; interstaminal glands rather indistinct, appearing as pale green scutiform patches at the very base of the corolla tube. Stamens included, the filaments inserted in the lower half or third of the tube, the wings 0.25 wide at the base; anthers short, oblong, 0.8 mm. long, 0.6 mm. wide, versatile. Pistil short-stipitate, the gynophore 0.3-0.5 mm. long; ovary elliptic-ovoid, 4-5 mm. long; stigmas sessile, elliptic, 0.5 mm. long, 0.3 mm. wide, erect. Mature capsule as long as the marcescent corolla or slightly exserted, dehiscent in the upper half. Seeds elongate-ovoid, about 1.2 mm. long, 0.7 mm. wide, very slightly flattened, minutely wrinkled under magnification, light brown.

Mountains of southwestern Utah and southern Nevada; along damp banks and on open hillsides and bare gravelly slopes among yellow pine at elevations of 2600-3300 meters; flowering from mid-July until late August; fruiting in September.

## UNITED STATES:

NEVADA: Clark Co.: Ridge to Charleston Peak, *Clokey 7625* (GH, MO, NY, US, WS); Rainbow Falls, *Clokey 8061* (NY); head of Lee Canyon, Charleston Mts., *Heller 11072* (GH, MO, NY, US).

UTAH: Garfield Co.: Bryce Canyon, *Eastwood & Howell 7230* (US); Panguitch Lake, *M. E. Jones 6008* (US). Iron Co.: Cedar Breaks, *Hitchcock, Rathke, & Van Raadsbooven 4586* (UC, WS). Kane Co.: 27 mi. s. Panguitch, *Maguire 19646* (WS).

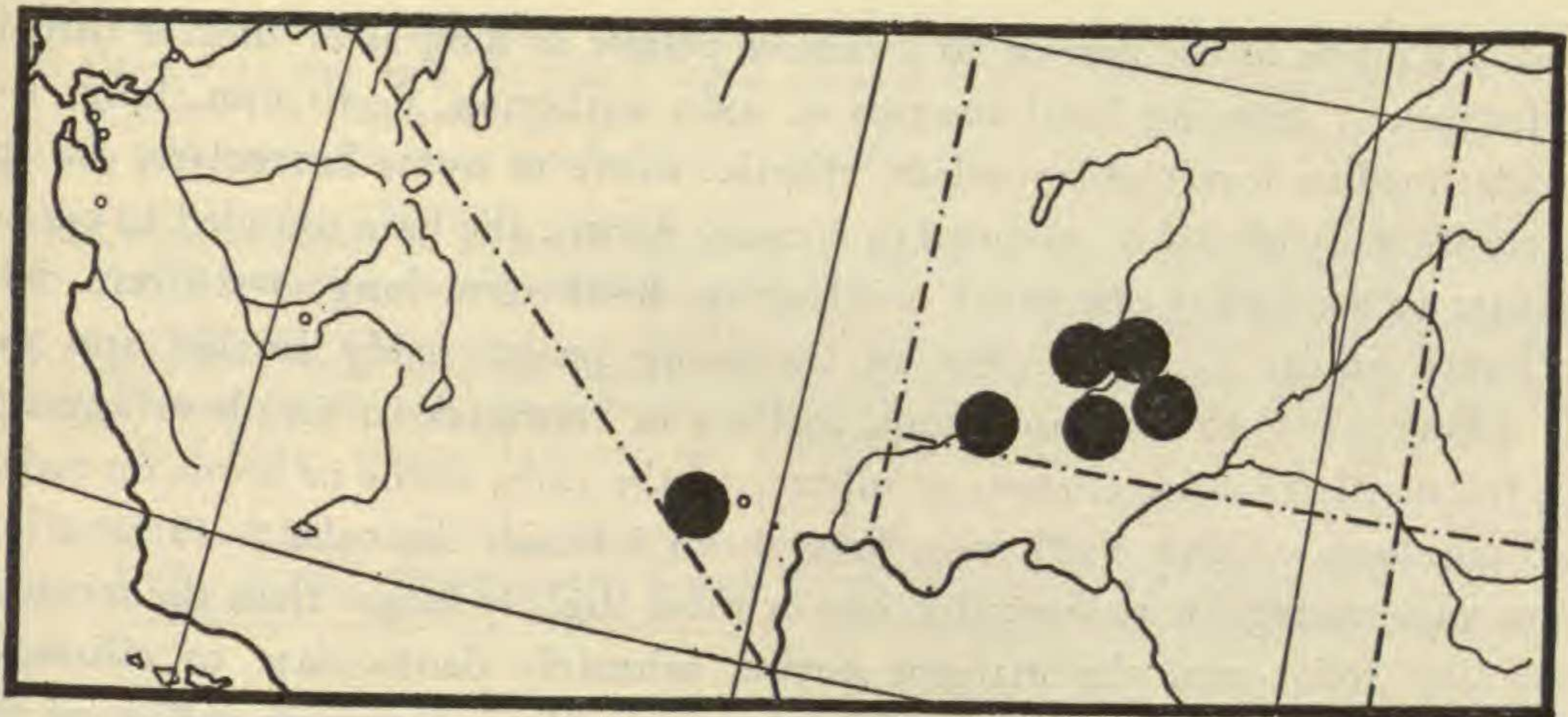


Fig. 6. Distribution of *Gentianella tortuosa* in Utah and Nevada.

*Gentianella tortuosa*, a very distinct species, appears to be rather localized since the collections came from only five localities. Distinctive field characters include the caespitose habit and the very numerous, somewhat campanulate flowers borne throughout the plant. The very long slender tap-root, sometimes twice as long as the aerial part of the plant, is a feature unique in this species.

The key appears to indicate a close alliance of *G. tortuosa* and *G. amarella* ssp. *acuta*. It would be unwise, however, to venture an opinion on relationships here, since the floral morphology, exclusive of size differences, is startlingly similar in many species of section AMARELLA, while in vegetative characters the plants are quite different. In floral morphology, *G. tortuosa* bears a great similarity to *G. aurea* of Greenland, except for the obvious expansion of the corolla itself and the presence of fimbriae in the throat. Since in so many instances in other species the presence or absence of fimbriae in the corolla orifice has proved to be an unreliable character, the presence of fimbriae should not be considered discordant. The ovoid ovary is a more reliable character to suggest affinity with *G. aurea*, since all other species within the section have distinctly cylindrical ovaries which are almost indistinguishable from one another except for size. Considering purely vegetative characters, the branching pattern of *G. tortuosa*, consisting as it does of many stems, suggests affinity with *G. amarella* ssp. *acuta*. The few fimbriae in *G. tortuosa* are hyaline and short, but although frequently found in two phalanges or groups on either side of the midvein, possess distinct vascular bundles.

11. GENTIANELLA AMARELLA (L.) Börner, Fl. deut. Volk, 543. 1912. (H. Smith in Hylander, in Uppsala Univ. Arssk. 259. 1945, superfluous comb.)

*Gentiana amarella* L. Sp. Pl. ed. 1, 230. 1753. (T.: Linn. Herb. 328.32, photo, A!)<sup>59</sup>

Annuals 5–70 cm. tall, simple or branched from the base or above, the basal branches occasionally bearing reduced flowers, the upper cauline branches frequently reduced. Basal leaves elliptic, lingulate to spatulate, the apex obtuse to

<sup>59</sup> Eurasian synonyms other than the basonym are not included here.

rounded, attenuate to the base or to a slender petiole as long as or shorter than the blade, frequently forming basal rosettes or soon withering, 3–40 mm. long, 1–11 mm. wide; median leaves oblanceolate, elliptic, ovate to ovate-lanceolate, the apex acute, occasionally obtuse or rounded in western forms, the base rounded to cordate, subconnate to somewhat decurrent or clasping, 8–60 mm. long, 3–20 mm. wide; upper leaves similar to the median or becoming progressively smaller and more acute. Flowers few to very numerous, axillary or terminal, in simple or aggregate cymes, frequently in dense clusters or solitary in the axils, sessile or borne on pedicels up to 5 cm. long. Calyx 5–25 mm. long, 4- to 5-lobed, the tube 2–40 mm. long, the lobes various, regular to irregular, one or more slightly larger than the remainder or becoming foliaceous, the margins entire, minutely denticulate to ciliate, the sinuses acute to somewhat rounded. Corolla white, blue, mauve, or yellow, or with a greenish tube, tubular, narrowly funnelform to salverform when the lobes are fully expanded, 10–25 mm. long, 2–6 mm. wide at the orifice, the lobes ovate to ovate-oblong, half the length of the tube, the tips obtuse to acute, the sinuses acute, the base of each lobe bearing a few to many slender fimbriae, free or united at the base to form a fimbriate scale; interstaminal glands at the base of the tube, scutiform. Stamens included, the filaments inserted in the lower half of the corolla tube, the wings 0.5–0.75 mm. wide at the base, slightly tapering above; anthers oblong, 0.75–1.5 mm. long. Pistil sessile or shortly stipitate, the gynophore up to 0.5–1.0 mm. long; ovary cylindrical to cylindrical-ovoid, about 8–15 mm. long, 1–4 mm. wide; stigmas sessile, elliptic to oblong, erect or recurved, 0.7–1.5 mm. long, 0.5–0.7 mm. wide. Capsule as long as the marcescent corolla or slightly exceeding it, dehiscent at the tip, the valves slightly spreading. Seeds variable, ovoid, slightly flattened, 0.5–1.0 mm. long, about 0.75–1.0 mm. wide, the surface smooth.

Throughout the northern temperate and arctic zones of Europe, Asia, and America, segregating into a large number of populations. In North America represented by five subspecies extending from the Arctic coasts and interior of Alaska to central Mexico; northeastward to Newfoundland and Maine, but not found in the greater Mississippi River basin nor in the eastern or southeastern United States.

The typical subspecies, *amarella*, occurs in central and western Europe and appears to be distinguished from *ssp. acuta* chiefly by its large flowers. Since *ssp. amarella* does not occur in North America, it is not described in this revision.

#### KEY TO THE SUBSPECIES

- a. One or more calyx lobes broadly foliaceous and enveloping the others; corona fimbriae united below to form a scale; stem with few (3–5) internodes; seeds about 1 mm. in diameter. Eastern and southern Utah and adjacent states.....11a. *G. amarella* *ssp. heterosepala*\*
- aa. Calyx lobes regular or irregular but never foliaceous; corona fimbriae free; stems with 5–12 or more internodes; seeds 0.75 mm. in diameter or less.
  - b. Lateral veins of the calyx lobes essentially parallel for some distance below the sinus, uniting towards the base of the tube. Highly variable subspecies with numerous local races. Newfoundland, Maine, and Vermont, westward to Alaska, southward in the western mountains to Baja California and central Mexico.....11b. *G. amarella* *ssp. acuta*\*



- bb. Lateral veins of the calyx lobes uniting immediately below the sinus.  
 c. Calyx 5–11 mm. long, the tube 2–3 mm. long, the lobes thinly membranaceous.  
 d. Flowers in simple or aggregate cymes or axillary branches, 8–12 mm. long, mauve, with essentially erect corolla lobes. Southern and central Mexico.....  
 .....11c. *G. amarella* ssp. *mexicana*  
 dd. Flowers chiefly in terminal umbelliform aggregate cymes, 9–17 mm. long, white, with spreading purple-speckled corolla lobes. North-central Mexico.....  
 .....11d. *G. amarella* ssp. *sandiana*  
 cc. Calyx 12–15 mm. long, the tube 3–4 mm. long, the lobes somewhat coriaceous.  
 e. Flowers 20–25 mm. long, frequently borne in compact clusters in the axils of upper leaves; plants 25–70 cm. tall. Northern Mexico and adjacent New Mexico.  
 .....11e. *G. amarella* ssp. *wrightii*  
 ee. Flowers 15–20 mm. long, in compact or loose clusters throughout the plant; plants 5–40 cm. tall. South-central Mexico in Michoacan and Mexico.....  
 .....11f. *G. amarella* ssp. *hartwegii*

\* *G. amarella* ssp. *heterosepala* grades into ssp. *acuta* with numerous intermediate forms.

11a. GENTIANELLA AMARELLA (L.) Börner, ssp. **heterosepala** (Engelm.) J. M. Gillett, comb. & stat. nov.

*Gentiana heterosepala* Engelm. in Trans. Acad. Sci. St. Louis 2:215. 1862. (T.: Engelm. s. n.!)  
*Gentiana distegia* Greene, Pittonia 4:182. 1900. (T.: Baker s. n.!)  
*Amarella heterosepala* (Engelm.) Greene, Leaf. Bot. Obs. & Crit. 1:53. 1904.  
*Amarella scopulorum* Greene, loc. cit. 55. 1904, ex char.  
*Gentiana polyantha* A. Nels. in Bot. Gaz. 56:68. 1913. (T.: Walker 513!)  
*Gentiana scopulorum* (Greene) Tidestrom, in Contr. U.S. Nat. Herb. 25:415–416. 1925.

Most common in Utah and extending into Colorado, Wyoming, New Mexico, Arizona and Idaho; in moist meadows and open aspen forests, from 2600 to 3200 meters; flowering from mid-July through August; fruiting from late August until September.

UNITED STATES:

- ARIZONA: Apache Co.: Hannagan Meadow, White Mts., Kearney & Peebles 12412 (US). Coconino Co.: Grand Canyon of the Colorado, MacDougal 173a (GH, US); San Francisco Mts., Lemmon & Lemmon s. n. (US).  
 COLORADO: Boulder Co.: Ward to Nederland, Weber 5734 (DAO). Delta Co.: Leroux Creek, Cowen 92 (GH). Dolores Co.: Ownbey 1478 (GH, MO, WS). Gunnison Co.: Gunnison Forest, Eggleston 14631 (GH, US). Mineral Co.: near Pagosa Peak, Baker s. n. (ND), Baker 518 (GH, MO, NY, US). Montrose Co.: Tabeguache Basin, Payson 169 (GH, MO). San Miguel Co.: Iron Springs Mesa, Walker 513 (GH, RM, WS).  
 IDAHO: Nez Perce Co.: Zaza, St. John & Muller 8634 (WS).  
 NEW MEXICO: Grant Co.: Black Range, Metcalf 1257 (GH, NY, US). Otero Co.: Sacramento Mts., Wootton s. n. (US). Rio Arriba Co.: Brazos Canyon, Standley & Bellman 10654 (US). Sandoval Co.: Sandia Mts., Ellis 225 (MO, NY, US). San Juan Co.: Tunitch Mts., Standley 7716 (US).  
 UTAH: Duchesne Co.: Cottonwood Canyon, Watson 942 (GH). Emery Co.: Muddy Creek region, Tidestrom 499 (US). Grand Co.: La Sal Mts., Payson & Payson 4073 (GH, MO). Iron Co.: Cedar Breaks National Monument, Gould 2051 (NY, US); Spring Lake, Parry s. n. (MO). Piute Co.: Tate Mine, Marysvale, Jones s. n. (US); Wasatch Mts., Jones 1138 (GH, NY). San Juan Co.: La Sal Mts., Purpus 7033 (MO, US). Sevier Co.: Fish Lake, Jones 5723 (MO, US). Summit Co.: Uintah Mts., Engelmann s. n. (MO), Payson & Payson 5067 (GH, MO, NY, US, WS). Utah Co.: Utah Lake, Parry 61 (MO, NY, US). Wasatch Co.: Clayton Peak, Wasatch Mts., Stokes s. n. (MO, US). Wayne Co.: Thousand Lakes Mountain, Fish Lake Nat. Forest, Johnson 81 (PH).  
 WYOMING: Big Horn Co.: Worthley 59 (US). Lincoln Co.: Cottonwood Lake, e. of Smoot, Payson & Armstrong 3765 (GH, MO).

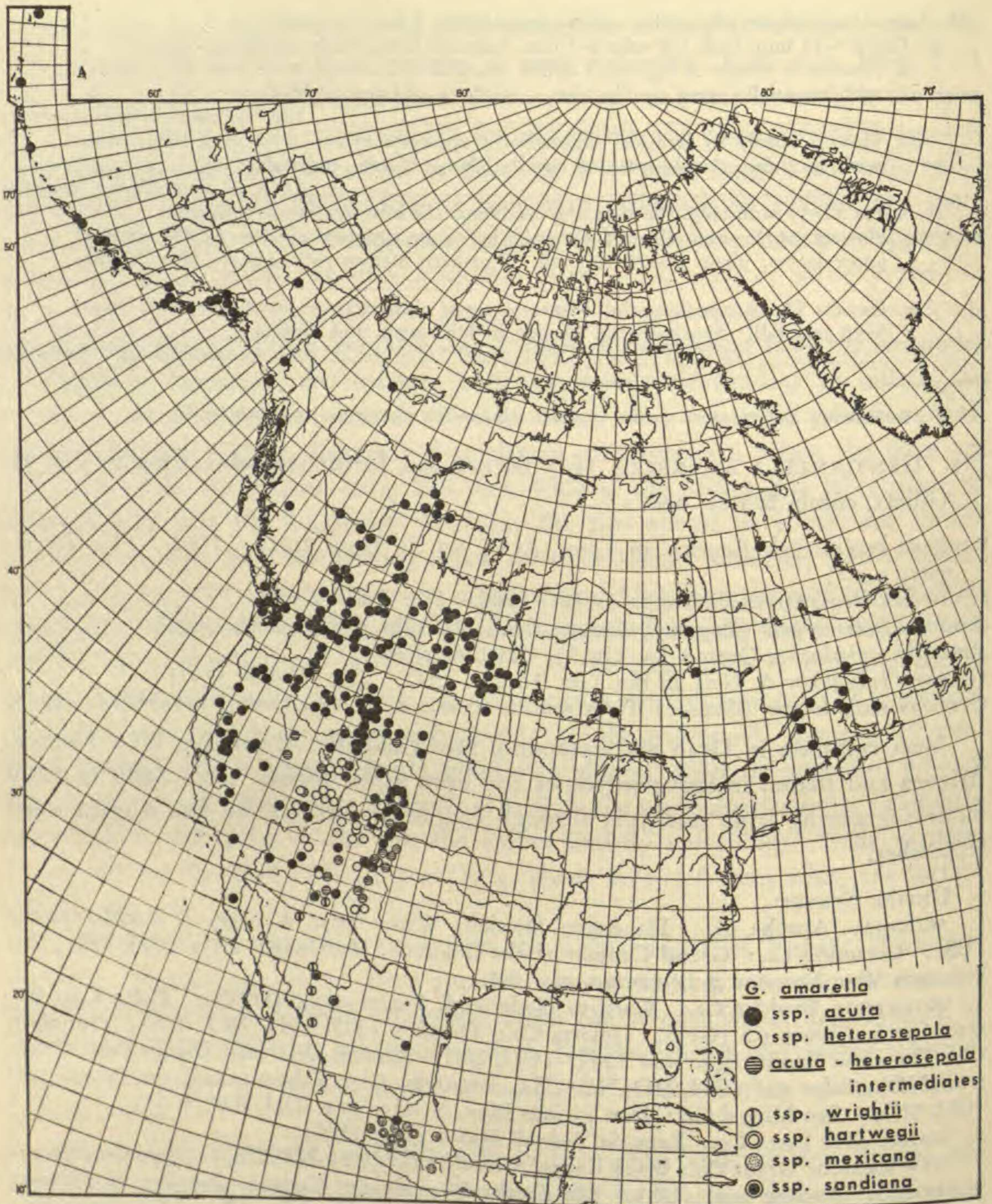


Fig. 7. Distribution of the subspecies of *Gentianella amarella* in North America.

Engelmann's *Gentiana heterosepala* is reduced to subspecific rank because neither the characters are sufficiently stable nor the range sufficiently isolated to warrant recognition as a species. A center of plants of somewhat pure ssp. *heterosepala* occurs in Utah, New Mexico, and Colorado. However, there are innumerable intergrades with ssp. *acuta* at the borders of its range. Plants of ssp. *acuta* throughout Wyoming and as far north as Montana show traces of *heterosepala* characters and various forms from this population have been described as species. Most of these I am placing in the synonymy of ssp. *acuta* since they lack the foliaceous calyx and many other characters of ssp. *heterosepala*. Undoubtedly this problem is too complex to solve completely by herbarium methods and it will be necessary to make further studies to define the groups properly.

The singular foliaceous calyx of ssp. *heterosepala* is paralleled in Europe by *G. campestris*. *Heterosepala* tendencies observed in this population include:

- |  |  |
|--|--|
| 1. Tendency toward larger flowers.   | 5. Larger, fewer seeds.  |
| 2. Enlargement of one or more calyx lobes.   | 6. Thickening of the stem.   |
| 3. Fewer stem nodes.   | 7. Larger cauline leaves accompanied by a trend from acute to obtuse leaves. |
| 4. Congestion of flowers by a shortening of lateral branches (var. <i>strictiflora</i> Rydb., a condition greatly affected by habitat conditions). | 8. Fusion of faucal fimbriae.  |
|  | 9. Congestion of the upper nodes   |
|  | 10. Trend from triangular to oblong calyx lobes.                             |

Shortening of upper internodes is a trend found also in *G. propinqua* and in *G. aurea*.

11b. GENTIANELLA AMARELLA (L.) Börner, ssp. *acuta* (Michx.) J. M. Gillett, comb. & stat. nov.

- Gentiana acuta* Michx. Fl. Bor. Amer. 1:177. 1803. (T.: Michaux s. n. photo MO!)
- Gentiana axillaris* Raf. Med. Fl. 1:213. 1828, ex char.
- Gentiana plebeja* Cham. ex Bunge, in Mem. Soc. Nat. Mosc. 7 (Nouv. Mem. Soc. Nat. Mosc. 1): 250. t. 29. f. 5. 1829, ex ic.
- Amarella acuta* (Michx.) Raf. Fl. Tellur. 3:21. 1837.
- Ericala acuta* (Michx.) G. Don, Gen. Syst. 4:190. 1838.
- Gentiana acuta* Michx.  $\beta$  *stricta* Griseb. Gen. & Sp. Gent. 242. 1839. (T.: Drummond s. n., photo MO!)
- Gentiana tenuis* Griseb. loc. cit. 250. 1839. (T.: Richardson s. n., photo MO!)
- Gentiana aggregata* Bunge, ex Griseb. in DC. Prod. 9:100. 1845, nom. nud. in syn.
- Gentiana acuta* Michx. var. *nana* Engelm. in Trans. Acad. Sci. St. Louis 2:214. 1862. (T.: Parry 309!)
- Gentiana amarella* L. var. *acuta* (Michx.) Herder, in Acta Hort. Petrop. 1:428. 1872.
- Gentiana amarella* L. var. *tenuis* (Griseb.) A. Gray, Syn. Fl. N. Amer. ed. 2, 2<sup>1</sup>:118. 1886.
- Gentiana anisosepala* Greene, Pittonia 3:309. 1898. (Heller & Heller 3440!)
- Gentiana acuta* Michx. ssp. *acuta* Wettst. in Oesterr. Bot. Zeitschr. 50:290. 1900.
- Gentiana acuta* Michx. ssp. *plebeja* (Cham.) Wettst. loc. cit. 194. 1900.
- Gentiana acuta* Michx. ssp. *plebeja* f. *holmii* Wettst. loc. cit. 195. 1900. (based on *G. acuta* var. *nana* Engelm.)
- Gentiana acuta* Michx. var. *strictiflora* Rydb. Mem. N. Y. Bot. Gard. 1:309. 1900. (based on *G. acuta*  $\beta$  *stricta* Griseb.)
- Gentiana stricta* (Griseb.) Howell, Fl. N.W. Amer. 1:445. 1901.
- Gentiana strictiflora* (Rydb.) A. Nels. in Bot. Gaz. 34:26. 1902.
- Gentianella clementis* Rydb. in Bull. Torr. Bot. Club 31:631. 1904. (T.: Clements & Clements 253!)
- Amarella anisosepala* (Greene) Greene, Leaf. Bot. Obs. & Crit. 1:53. 1904.

- Amarella conferta* Greene, loc. cit. 55. 1904. (T.: *Spreadborough s. n.*!)
- Amarella copelandi* Greene, loc. cit. 53. 1904. (T.: *Copeland s. n.*!)
- Amarella lemberti* Greene, loc. cit. 54. 1904. (T.: *Lembert s. n.*!)
- Amarella macounii* Greene, loc. cit. 54. 1904. (T.: *Macoun s. n.*!)
- Amarella revoluta* Greene, loc. cit. 55. 1904. (T.: *Wooton 552*!)
- Amarella strictiflora* (Rydb.) Greene, loc. cit. 53. 1904
- Amarella tenuis* (Griseb.) Greene, loc. cit. 53. 1904.
- Amarella amarella* (L.) Cockerell, in Am. Nat. 40:871. 1906.
- Amarella plebeia* var. *holmii* (Wettst.) Rydb. in Bull. Torr. Bot. Club 33:148. 1906.
- Amarella gurliae* Lunell, in Am. Midl. Nat. 2:142. 1911. (T.: *Lunell 816*!)
- Amarella theiantha* Lunell, loc. cit. 143. 1911. (T.: *Lunell 818*!)
- Amarella theiantha* Lunell var. *livida* Lunell, loc. cit. 142. 1913. (T.: *Lunell 820*!)
- Amarella theiantha* Lunell var. *lactea* Lunell, loc. cit. 1913. (T.: *Lunell 819*!)
- Gentiana amarella* L. f. *michauxii* Fern. in Rhodora 19:151. 1917. (based on *G. acuta* Michx., sensu stricto)
- Gentianella acuta* (Michx.) Hiit. in Mem. Soc. Faun. Fl. Fenn. No. 25:76. 1950.

Newfoundland, Maine and Vermont, westward to Alaska, southward in the western mountains to Baja California and central Mexico.

Some of the large number of reported habitats with flowering dates and elevations, are as follows:

*Alaska*: Rocky shores, sand-dunes, sea-beaches, tundras, lake shores, moist grassy swales, apparently at rather low altitudes; flowering and fruiting from June to September.

*Alberta*: Roadsides, open poplar woods, alkaline meadows, dry prairies, mountain slopes, sides of coulees; late July until September.

*Quebec*: Wet fields, calcareous gravel, limestone, turfy slopes, sandy headlands, above the tide mark, near sea-level; late June to early September.

*Wyoming*: Along creeks, open woods, alpine meadows, alkali areas up to 3000 meters; late July and throughout August.

*California*: Grassy banks, poplar woods, grassy places in yellow pine forest, to 2500 meters; early June to September dependent upon altitude.

*Arizona*: Dry or moist meadows to 3500 meters; flowering and fruiting from mid-August until September.

#### CANADA:

**ALBERTA**: Lake Louise, *Brown 546* (GH, MO, PH, US); Bow Lake, Banff Nat. Park, *Hitchcock & Martin 7791* (plants 1, 3, 4, 6, & 7 GH); Banff to Field, *Schaffer s. n.* (PH); Cypress Hills, Spring Creek, *Breitung 5518* (DAO, MO); Elkwater Lake, *Breitung 5547* (DAO); Craigmyle District, *Brinkman 267* (NY), *292* (DAO); Twin Butte, *Gillett 6023* (DAO); Keg River, *Grob 2934* (DAO); Mt. Temple, Loggan, *Butters, Holway & Rosendahl 305* (GH, NY, US); Pincher Creek, *Gillett 6026* (DAO); Waterton Lakes Nat. Park, *Gillett 6029* (DAO); Crow's Nest Pass, *Macoun s. n.* (US); Wood Buffalo Park, Moose (Eight) Lake, *Raup 3030* (CAN, GH, US), *3031* (CAN); Hay Camp Dist. Slave River, *Raup 3032* (CAN, GH); Brasean, headwaters Saskatchewan and Athabasca rivers, *Brown 1435* (GH, MO, PH); Fort Chipewyan, *Raup 7028* (GH); Jasper Nat. Park, *Riley 6* (US); Devona, *Scamman 3153* (GH, US); Fort Saskatchewan, *Turner 2118* (DAO); Beaverlodge, *Lindsay 303* (DAO); Grande Prairie, *Malte 40* (CAN); Edmonton, *Malte s. n.* (CAN); Caribou Mountains, *Raup 3035* (CAN); Rosedale, *Moodie 1209* (F); Peace River, Indian Graveyard, *Raup 3036* (CAN); Lake Mamawi, *Raup 3037* (CAN).

**BRITISH COLUMBIA**: Victoria, *Fletcher s. n.* (DAO); Apex Mountain near Hedley, *Gillett & Senn 6053* (DAO); Prince George, *Grob 636* (DAO); Hudson Hope, Peace River Dist., *Grob 745* (DAO); Skaget, *Davidson s. n.* (UBC); Victor Lake, near Revelstoke, *Hitchcock & Martin 7575* (GH, NY, WS); Kettle and Columbia rivers, *Macoun*

*s. n.* (WS); Cassiar Dist., Telegraph Creek, *Preble & Mixter 577* (US); Mt. Robson, *Scammon 3322* (GH, US); Selkirk Mts., *Shaw 180* (GH, MO, US, WS); Caribou, 150 Mile House, *Wilson 717* (UBC); Foghorn Mt. s. of Waverly, *Tisdale s. n.* (DAO); Tranquille Range, Kamloops, *Tisdale 40-621* (DAO); Elk River, Natal, *Weber 2301* (WS); nr. Cranbrook, *Calder & Savile 9169* (DAO); Okanagan, Allen Grove, *Copley 22* (UBC); between Moyie & Cranbrook, *Eastham 15373* (UBC); Fermie, *Eastham 15695* (UBC); Colleymount, François Lake, *Eastham 11907* (UBC); Anahim Lake, Chilcote, *Cornwall s. n.* (UBC); Paradise Mine, Windermere, *Calder & Savile 11300* (DAO); Takakkaw Falls, Yoho River Valley, *Calder & Savile 12016* (DAO); Chute Lake, Naramata, *Calder & Savile 10202* (DAO); Cascade, *Calder & Savile 9539* (DAO); Quesnel, *Taylor s. n.* (UBC); Fairmont Hot Springs, *Eastham 10137* (UBC); Williams Lake, Dog Creek Range, *Carlyle s. n.* (UBC); Queen Charlotte Islands, Massett, *Newcombe s. n.* (F); Nakina Lake, Atlin Dist., *Aitken 39* (DAO); Topley, *Calder, Savile & Ferguson 14535* (DAO); Wells, *Calder, Savile & Ferguson 14193* (DAO); Kispiox River, n. Hazelton, *Calder, Savile & Ferguson 14751* (DAO); Azousetta Lake, *Calder, Savile & Ferguson 13996B* (DAO); Ft. St. James, *Calder, Savile & Ferguson 13622* (DAO); Mt. Pope, *Calder, Savile & Ferguson 13799* (DAO); Hudson Bay Mountain, Smithers, *Calder, Savile & Ferguson 14668* (DAO).

LABRADOR: Blanc Sablon, Straits of Belle Isle, *Fernald & Wiegand 3905* (GH); Cartwright, *Hitchcock 23845* (US); L'Anse au Clair, *Wagborne 2* (US).

MACKENZIE DISTRICT: Lac Ste. Croix and Bear Lake, *Preble 268* (US); Fort Smith, *Preble & Preble 171* (US); Yellowknife, *Cody & McCause 3246* (DAO); Little Buffalo River, *Loan 327* (DAO); Seven Mile Lake, *Cody & Loan 4661* (DAO).

MANITOBA: Lyleton, *Boivin & Breitung 6588* (DAO); Turtle Mt., *Burgess s. n.* (DAO); Brandon, *Macoun s. n.* (F); Winnipeg, *Denike 1689* (DAO); Wabowden Lake, Mile 137 Hudson Bay R.R., *Gillett 2775* (DAO); Dauphin, *Grob s. n.* (DAO); Stony Mountain, *Grob s. n.* (DAO); Riding Mountain Nat. Park, *Rowe 60A* (DAO); Cartwright, *Senn & Gordon 3036* (DAO); Broomhill, *Senn & Gordon 3120* (DAO); Melita, *Senn & Gordon 3102* (DAO); Chaplin, *Spreadborough s. n.* (ND).

NEW BRUNSWICK: Gloucester Co.: Grande Plaine, Miscou Island, *Blake 5594* (GH, US), *Ganong s. n.* (GH); Goat Island, mouth of St. John River, *Hay s. n.* (PH).

NEWFOUNDLAND: Cartierville, *Bassett 715* (DAO); St. Barbe, *Fernald, Long, et al. 26972* (GH, PH); Ingornachoix Bay, *Fernald & Wiegand 3902* (GH, PH); St. Anthony Bight, *Savile 2925* (DAO); St. John Bay, Bard Harbour, *Wiegand & Gilbert 28931* (GH, PH).

ONTARIO: Schreiber, Lake Superior n. shore, *Dore 9236* (DAO); St. Ignace Islands, Lake Superior, *Smith s. n.* (PH).

QUEBEC: Fort Chimo, *Calder 2412* (DAO, US); Anticosti, Baie Sainte-Claire, *Victorin 4290* (MO, US); Rivière au Saumon, *Victorin et al. 21064* (F); Bonaventure Co.: *Williams & Fernald s. n.* (US). Gaspé Co.: Paspébiac, *Churchill s. n.* (MO); James Bay, Fort George, *Lepage 12851* (DAO); Rupert House, *Spafford 160* (DAO); Temiscouata, *Pringle s. n.* (F, MO, PH, US); Douglstown, *Collins & Pease 6605* (F); Magdalen Islands, Coffin Island, *Fernald, Long & St. John* (PH, US, WS); Mingan Islands, Île de Sainte-Genevieve, *Victorin & Rolland 21063* (GH, MO, PH); Rivière du Loup, *Canby s. n.* (F).

SASKATCHEWAN: Springside, *Blaricom 26* (F); Carleton House to Cumberland House, *Drummond s. n.* (GH); Cypress Hills, Fort Walsh, *Breitung 5685* (DAO, MO); Moose Jaw, *Barber 30* (GH); Saskatoon, *Macoun & Herriot s. n.* (GH); Lake Athabasca, *Raup 6591* (GH); Regina, *Cowdry s. n.* (DAO); Watrous, *Sallans & Russell s. n.* (DAO); Yorktown, *Shaw 157* (DAO); Sutherland, *Russell s. n.* (DAO); McKague, *Breitung 476* (DAO); Invermay, *Russell 51794* (DAO); St. Louis, *Senn, Grob & Russell 2838* (DAO); Manitou Lake, *Frankton & Bibbey 413* (DAO); Bjorkdale, *Laycock s. n.* (DAO); Prince Albert, *Senn, Grob & Russell 2817* (DAO); Willowbunch, *Gillett & Boivin 6013* (DAO); Bengough, *Gillett & Boivin 6010* (DAO); Whitewood, *Gillett & Boivin 6001* (DAO); Ile à la Cross, Churchill River, *Breitung 8427* (DAO); Kennedy, *Gillett & Boivin 6002*; Macdowall, *Senn, Grob & Russell 2898*, (DAO); Rockglen, *Gillett & Boivin 6018* (DAO).

YUKON: Dawson, *Macoun s. n.* (NY); Bear Creek near Lake Desert d'Asch, *Müller s. n.* (PH, US).

## UNITED STATES:

ALASKA: Fort Yukon, *Kennicott s. n.* (F); Hiulink, *Harrington s. n.* (US); Unalaska, *Harrington s. n.* (MO); Fairbanks, *Palmer 1826* (US); Spruce Island, *Kellogg 246* (PH, US); Juneau, *Cowles 1096* (F, GH, MO, US); Karluk, Kodiak Island, *Rutter 71* (GH, NY, US); Homer, *Evans 499* (US); Dutch Harbor, Unalaska Island, *True & Prentiss 129* (US); Lake Kenai, Kenai Peninsula, *Calder 5587, 6335* (DAO); Cape Phipps, *Funston 72* (F, GH, MO, US); Katmai Region, Alaska Peninsula, *Hagelbarger 165* (US); Attu Island, Sarana Bay, *Van Schaack 1000* (MO, US); Behring Island, *Macoun s. n.* (US); Alitak, *Looff & Looff 774* (UBC); Adak Island, *Dorwart 45* (F); Dauer Bay, *Cooper & Andrews 313* (F).

ARIZONA: Apache Co.: White Mts., *Eggleston 15771* (F, GH). Coconino Co.: Kaibab Forest, Grand Canyon Park, *Kearney & Peebles 13727* (US). Graham Co.: Pinaleno Mts., Darrow, *Phillips & Putz 1106* (US). Yavapai Co.: *Lemmon 4200* (GH). Yuma Co.: Buckskin Mts., *Jones 6056n* (US).

CALIFORNIA: Butte Co.: Butte Meadows, *Heller 14689* (MO, NY, US); Jonesville, *Copeland 441* (F). Inyo Co.: Whitney Meadows, *Coville & Funston 1631* (US). Mariposa Co.: Tuolumne, Yosemite Nat. Park, *Heller 15464* (MO, NY, PH, US). Mono Co.: Bloody Canyon, *Chesnut & Drew s. n.* (US). Nevada Co.: *Williamson s. n.* (PH). Placer Co.: Summit Station, *Sonne s. n.* (US); Truckee, *Sonne 217* (F). San Bernardino Co.: Pine Lake, *Abrams 2897* (GH, MO, PH, US). Plumas Co.: *Austin s. n.* (US); Bear Lake, *Clokey 7000* (F). Shasta Co.: *Newberry s. n.* (US). Sierra Co.: *Lemmon 190* (NY). Siskiyou Co.: Mount Eddy, *Copeland s. n.* (ND). Tuolumne Co.: Tuolumne River, *Bolander 5045* (F, MO, NY, PH, US); Yosemite Valley, *Lembert s. n.* (ND). Tulare Co.: Kern River, *Greene 4241* (GH, NY).

COLORADO: Boulder Co.: Boulder, *Holzinger s. n.* (US). Chaffee Co.: Garfield, *Eggleston 6068* (GH, US). Clear Creek Co.: Georgetown, *Patterson 287* (F, GH, MO, US). Custer Co.: Wet Mountain Valley, *Horner s. n.* (GH). Denver Co.: *Glatfelter s. n.* (MO). Eagle Co.: Leadville Forest, *Eggleston 11842* (US). El Paso Co.: Minnehaha, *Clements & Clements 253* (GH, MO, NY, US); Pike's Peak, *Spruce s. n.* (F). Fremont Co.: Grape Creek, *Demitrio s. n.* (GH). Garfield Co.: White River Plateau, *Hermann 5580* (MO). Gilpin Co.: Black Hawk, *Sheldon 286* (PH, US). Grand Co.: Berthoud Pass, *Clokey & Clokey 4241* (CAN, MO, UC, US, WS). Gunnison Co.: Gunnison, *Baker 600* (GH, MO, US, WS). La Plata Co.: Durango, *Baker et al. 629* (MO, NY, US). Routt Co.: Steamboat Springs, *Crandall s. n.* (US). Hinsdale Co.: Lake City, *Pease s. n.* (NY). Jackson Co.: Lake John, *Shear & Bessey 4335* (US). Jefferson Co.: Golden, *Greene s. n.* (GH). Lake Co.: Twin Lakes, *Clokey 2548* (CAN, MO, NY, US, WS). Larimer Co.: Chamber's Lake, *Baker s. n.* (MO, NY, US). Mineral Co.: *Murdock 4842* (MO, NY). Ouray Co.: Ouray, *Evermann s. n.* (US). Park Co.: Jefferson, *Cowen 1502* (CAN, US, WS). Pitkin Co.: Sawatch Range, *Brandeggee s. n.* (MO). Rio Blanco Co.: North Elk Canyon, *Sturges s. n.* (GH). Rio Grande Co.: Del Norte, *Evermann s. n.* (US). Saguache Co.: Marshall Pass, *Baker 885* (GH, MO, US). San Juan Co.: Head of Vallecito, *Knowlton 44* (US). San Miguel Co.: Trout Lake, *Payson & Payson 4117* (GH, MO). Summit Co.: Breckenridge, Mt. Guyot, *Anderson s. n.* (MO). Location unknown: *Parry 309* (GH, MO, NY).

IDAHO: Blaine Co.: Hyndman Creek, *Thompson 13520* (PH, MO, US, WS). Boise Co.: Warm Springs Creek, *Woods & Tidestrom 2709* (US). Boundary Co.: Hughes Fork Trail, *Warren 368* (WS). Custer Co.: Bonanza, *Macbride & Payson 3475* (GH, MO, US). Fremont Co.: Henry's Fork, *Coulter s. n.* (PH, US). Kootenai Co.: Lake Cœur d'Alene, *Aiton s. n.* (F, MO, US). Latah Co.: Cedar Mts., *Sandberg & MacDougal 424* (F, GH, MO, PH, US); Moscow Mountain, *Baker 134* (ID), *Thomas s. n.* (ID). Lemhi Co.: Challis, *Hitchcock & Mublick 11346* (GH, NY, US, WS). Nez Perce Co.: Forest, *Heller & Heller 3440* (DAO, MO, ND, NY).

MAINE: Aroostook Co.: St. John River, Van Buren, *Fernald s. n.* (GH); St. John River, St. Francis, *Fernald 85* (CAN, F, GH, MO, PH, US); Houlten, *Fubish s. n.* (GH).

MONTANA: Beaverhead Co.: Pioneer Range, *Hitchcock & Mublick 13030* (GH, MO, UC, WS). Carbon Co.: Red Lodge, *Hitchcock & Mublick 13554* (WS). Flathead Co.: Big Fork, *Jones s. n.* (GH, MO, US). Gallatin Co.: Gallatin Canyon, *Blankinship 349* (PH, US); Glacier Co.: 3 mi. s. Babb, *Daubenmire 48381* (WS); Glacier Nat. Park,

Bowman, *Evans s. n.* (F). Granite Co.: Garnet, *Scheuber s. n.* (NY). Lake Co.: Big Fork, *Clemens s. n.* (GH). Lewis & Clark Co.: Flathead Nat. Forest, *Hitchcock 18743* (WS). Madison Co.: Ennis, *Hitchcock 16736* (UC, WS). Meagher Co.: Martinsdale, *Canby s. n.* (F, PH, MO). Missoula Co.: Woodman, *Kirkwood 1475* (GH). Park Co.: Wilsall, *Suksdorf 87* (GH, WS). Powell Co.: Flathead Nat. Forest, *Hitchcock 18549* (ID, WS). Sweet Grass Co.: MacLeod, *Pope 105* (NY). Teton Co.: Glacier Nat. Park, *Hunnewell 2158* (GH).

NEVADA: Elko Co.: Ruby Valley, *Heller 9467* (US).

NEW MEXICO: Catron Co.: Mogollon Peak, *Eggleston 16931* (US), *Rusby 262* (F). Colfax Co.: Castle Rock, *Wooton s. n.* (US). Lincoln Co.: White Mts., *Wooton 552* (MO, US). Sandoval Co.: Jemez Mts., *Bailey 1026* (US). San Miguel Co.: Pecos, *Standley 5011* (GH, MO, US). Santa Fe Co.: *Bertaud 24* (US). Taos Co.: Carson Forest, Apache Peak, *Eggleston 19200* (US).

NORTH DAKOTA: Benson Co.: Leeds, *Lunell 816* (MIN, NY), *Lunell 818* (MIN); Butte, *Lunell 820* (MIN). Bottineau Co.: Turtle Mts., *Stevens 540* (DAO, MO, US). Divide Co.: Fortima, *Metcalf 597* (US). McHenry Co.: Tower, *Lunell 819* (MIN).

OREGON: Crook Co.: Pengra, *Coville & Applegate 541* (US). Deschutes Co.: Big Meadows, *Leiberg 496* (GH, MO). Jefferson Co.: Metoline River, *Gorman 3887* (WS). Klamath Co.: Fort Klamath, *Peck 9557* (MO, PH). Union Co.: Blue Mts., *Cusick 1029* (GH, US); Wallowa Mts., *Cusick 2101* (F, MO, US, WS).

SOUTH DAKOTA: Custer Co.: Custer, *Degener & Peiler s. n.* (MO, US). Lawrence Co.: Lead, *Carr 144* (DAO, GH, MO). Pennington Co.: Redfern, *Murdoch 4285* (GH, US); Mystic, *Visser s. n.* (F).

UTAH: Beaver Co.: Tashar Mts., *Eggleston 10417* (US). Cache Co.: Tony Grove Lake, *Maguire 16996* (WS). Duchesne Co.: Krobs Basin, *Hermann 5190* (GH, MO). Garfield Co.: Aquarius Plateau, *Ward 440* (MO, US). Kane Co.: *Siler s. n.* (MO). Salt Lake Co.: Brighton, *Maguire 17317* (US, WS). Sanpete Co.: *Watson 59* (ID). Sevier Co.: Fish Lake, *Jones 5823* (GH, MO, NY, US, WS). Washington Co.: Springdale, *Jones 6078* (MO).

VERMONT: Lamoille Co.: Mt. Mansfield, Smuggler's Notch, *Pringle in 1871* (MO, NY, PH, US); and many other collections in most American herbaria.

WASHINGTON: Clallam Co.: Mt. Angeles, *Thompson 7357* (GH, MO, PH). Ferry Co.: Coville, *Hitchcock 17607* (DAO, ID, US). Jefferson Co.: Olympic Mts., Marmot Pass, *Thompson 7988* (GH, MO, PH). King Co.: Seattle, *Freiberg s. n.* (MO). Okanogan Co.: Salmon Meadows, *Thompson 6943* (GH, MO). Pend Oreille Co.: *St. John 6462* (WS). San Juan Co.: Friday Harbor, *Zeller & Zeller 918* (GH, MO, US). Skagit Co.: Dewey, *Mason s. n.* (WS). Stevens Co.: Arden, *Spiegelberg 267* (WS). Whatcom Co.: Padden Lake, *Suksdorf 990* (F, GH, MO, US, WS).

WYOMING: Yellowstone Nat. Park, Snake River, *Nelson & Nelson 6447* (GH, MO, US, WS). Albany Co.: Centennial, *Nelson 8803* (GH, MO, US). Big Horn Co.: Middle Ten Sleep Creek, *Goodding 471* (GH, US). Carbon Co.: Rawlins, *Goodding 570a* (MO, US). Park Co.: Beartooth Lake, *Williams & Williams 3755* (GH, MO, NY). Shoshone Co.: 21 mi. from Cooke City, *Iltis 3996* (DAO). Sheridan Co.: Spring Creek, *Williams & Williams 3362* (GH, MO, NY). Sublette Co.: Surveyor Park, Fremont Lake, *Payson & Payson 2903* (GH, MO, US). Teton Co.: Teton Mts., *Porter 4741* (DAO). Uinta Co.: Mt. View, *Maguire, Piranian & Richards 12643* (GH). Washakie Co.: Big Horn Mts., *Porter 4343* (GH, MO). Weston Co.: Newcastle, *Nelson 2551* (F).

#### MEXICO:

BAJA CALIFORNIA: La Sanca Creek, 5 mi. n.w. La Grulla Sierra, San Pedro Martir, *Wiggins & Demaree 4845* (F, GH); La Encantada nr. Vallecitos, Sierra San Pedro Martir, *Wiggins 9075* (GH, US).

MÉXICO: Nevada de Toluca, *Moore 89a* (GH), *Kenoyer s. n.* (F).

NUEVO LEON: Municipio de Galeana, peak of Cerro Potosi, *Schneider 971* (F, GH), *Mueller 2247* (F, GH).

For the combination *Gentianella amarella* (L.) Börner and other Börner references I am indebted to Dr. Harald Smith, of Uppsala, who pointed out to me that Börner had made the combination earlier in his Flora. This Flora, although recent, is not widely distributed on this side of the Atlantic. The Library of Congress has a copy but I know of no other in the United States.

*G. amarella* ssp. *acuta* is extremely variable, particularly in the number of internodes, the size and shape of the calyx lobes, the length of the corolla tube and lobes, and the density of the inflorescence. Field observations indicate that great variability in height of the plant, density of the inflorescence, color of the flowers, and other features is found in local populations as well as in groups of plants of the range as a whole. The pattern of this variability is not sufficiently well understood at this time to warrant the recognition of additional forms or subspecies.

It has been necessary to establish the relationship of ssp. *acuta* to the European population of *Gentianella amarella* (*sensu lato*). The few European specimens of *G. amarella* that I have seen show an astonishingly great variability. Many "species" have been based upon the variants of this European population; many of them are difficult to distinguish morphologically, and perhaps should be reduced to subspecific or lesser rank. Most of the typical specimens of the European *G. amarella* have somewhat larger flowers than do the American plants of ssp. *acuta*. Since *G. amarella* does not occur in Greenland, the American and the European populations are disjunct. Because of this geographic disjunction and the difference in flower size, I am recognizing the American population as subspecifically distinct from typical *G. amarella* of Europe.

The few specimens I have seen from Siberia and other parts of Asia show close resemblance to *G. amarella* ssp. *acuta*. These Asiatic plants have been described under the name *Gentiana ajanensis* by Murbeck.<sup>60</sup> However, I shall not consider the Asiatic population as synonymous with ssp. *acuta* until I have seen more material from that region.

11c. GENTIANELLA AMARELLA (L.) Börner, ssp. *mexicana* (Griseb.) J. M. Gillett, comb. & stat. nov.

*Gentiana mexicana* Griseb. Gen. & Sp. Gent. 243. 1839, ex char. (T.: *Schiede s. n.*)  
*Amarella mexicana* (Griseb.) Arthur, in *Torrey* 12:34. 1912.

Southern and central Mexico; in wet meadows and on gravelly slopes near timber-line and along creek banks at elevations of 2000–3000 meters. Flowering from mid-September through October; fruiting in October and November.

MEXICO:

FEDERAL DISTRICT: south of Contreras, *Russell & Souviron 197* (US); Desierto de los Leones, *Lyonnet 517* (GH, MO, NY, US); La Cima, 9800 ft., *Barnes & Land 383* (F).

HIDALGO: Pachuca District, Mineral del Chico, Parque Nacional El Cluco, *Moore 1607* (GH).

MEXICO: Temascaltepec, *Hinton 8313* (F, GH, MO, NY, US); Crucero-Agua Blanca, Temascaltepec, *Hinton 8330, 2117* (F, GH, MO, NY, US); Sierra de las Cruces, *Pringle 4277* (F, MO, NY, PH, US).

<sup>60</sup> Murbeck, in *Acta Hort. Berg.* 2<sup>3</sup>:1–28. 1892.



OAXACA: Sierra de Calvellinas, 9000 ft., Smith 667 (MO, US).

PUEBLA: Ixtaccihuatl, Purpus 1757 (F, MO, US).

VERACRUZ: Cofre de Perote, 9300 ft., Balls 5435 (US).

LOCALITY UNKNOWN: Ehrenberg 79 (GH).

11d. *GENTIANELLA AMARELLA* (L.) Börner, ssp. *sandiana* J. M. Gillett, subsp. nov.

Plantae 2.0–3.5 dm. altae ramosae. Folia basalia elliptica vel spatulata 4–10 mm. longa jam marcida superiora ovata vel ovato-lanceolata, 10–25 mm. longa 5–10 mm. lata, acuta. Flores numerosi, 9–17 mm. longi, aut infundibuliformes aut hypercrateriformes cum lobis maxime dilatatis sessiles aut pedicellis ca. 8 mm. longis in cymis terminalibus axillaribusve dense aggregatis umbelliformibus vel corymbiformibus. Calix 5–17 mm. longus, tubo 2.0–2.8 (–3.0) mm. longo, lobis lineari-oblongis acutis subaequalibus quam tubo aliquantum longioribus sinibus rotundatis margine minute denticulato. Corolla alba 10–15 mm. longa lobis albis aut purpureo-maculatis basim fimbriatis. Anthera 1 mm. longa 0.5 mm. lata. Ovarium sessile ca. 12 mm. longum 1.5 mm. latum; stigmata oblonga patula vel erecta ca. 0.5 mm. longa. Semina immatura rotundata laevia maturitate ignota.

Restricted to Chihuahua and Durango. Habitat probably similar to that of *G. wislizeni* for some material is from the same locality. At an altitude of about 2500 meters, flowering in October.

MEXICO:

CHIHUAHUA: Palmer 334 (GH, NY, US); 65 mi. east of Batopilas, Goldman 188 (US).

DURANGO: Mesa de Sandia, Pringle 10111 (F, GH, MEXU, MO HOLOTYPE, NY, US).

Very similar to *G. wislizeni* in many respects but having a distinctly tubular calyx. The dense terminal corymbs of fimbriate flowers with the speckled corolla lobes are striking features of this subspecies.

11e. *GENTIANELLA AMARELLA* (L.) Börner, ssp. *wrightii* (A. Gray) J. M. Gillett, comb. & stat. nov.

*Gentiana wrightii* A. Gray, Syn. Fl. N. Amer. ed. 2, 2<sup>1</sup>:118. 1886. (T.: Wright 1659!)

*Amarella wrightii* (A. Gray) Greene, Leaflet Bot. Obs. & Crit. 1:53. 1904.

*Amarella cobrensis* Greene, loc. cit. 56. 1904. (T.: Greene s. n.!)

*Gentiana townsendii* Briq. in Candollea 4:329. 1931. (T.: Townsend & Barber 358!)

Northern Mexico and in adjacent New Mexico; flowering from late August until the middle of November, at altitudes of 2100–2400 meters, in moist and springy places.

UNITED STATES:

NEW MEXICO: Grant Co.: Pinos Altos Mts., Greene s. n. (F, MO, NY, PH).

MEXICO:

CHIHUAHUA: Sierra Madre, Jones s. n. (MO, US); southwest Chihuahua, Palmer 306 (F, GH, MO, US); near Colonia Garcia, Townsend & Barber 358 (F, GH, MO, NY, US); Pennell 18744, 19116 (US).

SINALOA: Cerro del Viejo, San Ignacio, Montes & Salazar 83 (US).

SONORA: Santa Cruz, Wright 1659 (GH, MO, NY, PH, US).

LOCALITY UNKNOWN: Cima, Orcutt 3800 (F).

Subspecies *wrightii* is extremely variable. Greene's *Amarella cobrensis* is very similar to the material collected by Wright. *Gentiana townsendii* appears to be but a form with exceptionally dense axillary inflorescences. Since so little material of *G. townsendii* is available, I do not feel that much significance can be attached to this variation, because the flowers appear to be identical in every respect to other sheets of ssp. *wrightii*.

*Gentianella amarella* ssp. *hartwegii* and *G. amarella* ssp. *wrightii* are related to the more northern *G. amarella* ssp. *acuta*, but are distinguishable quite easily by the longer calyx tube and the nature of the lobes. The calyx lobes of ssp. *acuta* are thin, as are those of ssp. *wrightii*, and the margins are little differentiated from the central part of the lobe. In ssp. *acuta* the midrib of each lobe is not prominent and appears as a thin nerve. In ssp. *hartwegii*, however, the lobes are somewhat coriaceous, the margins somewhat thickened, and the midrib of each lobe broad and papillose, forming a flattened keel which extends the length of the calyx tube and is paralleled by a similar keel proceeding from the sinus. The midribs of the calyx lobes of ssp. *wrightii* are intermediate between those of ssp. *acuta* and ssp. *hartwegii*.

11f. GENTIANELLA AMARELLA (L.) Börner, ssp. *hartwegii* (Benth.) J. M. Gillett, comb. nov.

*Gentiana hartwegii* Benth. Pl. Hartw. 47. 1840. (T.: *Hartweg 351*, photo MO!)

*Gentiana citrina* Pollard, in Proc. Biol. Soc. Wash. 13:130. 1900. (T.: *Pringle 4196!*)

*Gentiana mexicana* Griseb. ssp. *hartwegii* (Benth.) Wettst. in Oesterr. Bot. Zeitsch. 50:291. 1900.

*Gentiana mexicana* ssp. *hartwegii* f. *pringlei* Wettst. loc. cit. 291. 1900. (T.: *Pringle 4237!*)

*Amarella hartwegii* (Benth.) Arthur, in Torreyia 12:33. 1912.

In the states of Mexico and Michoacan, Mexico; in wet mountain meadows at altitudes of 2800–3300 meters; flowering from mid-August until October; fruiting in October and November.

MEXICO:

MEXICO: Nevado de Toluca, *Kenoyer A357* (F); Temascaltepec, *Hinton 1317, 8320* (F, GH, MO, US); Valley of Toluca, *Pringle 4196* (F, GH, MEXU, MO, NY, US), *Pringle 4237* (F, GH, MO, US); Desierto Vieja, Valée de Mexico, *Bourgeau 1125* (GH).

MICHOACAN: Anganguero, *Hartweg 371* (NY, photo F, MO).

LOCALITY UNKNOWN: *Sessé, Mociño, Castillo & Maldonado 684, 1370* (F).

Wettstein considered ssp. *hartwegii* a subspecies of *G. mexicana*. While all of the Mexican plants are very closely related I believe that ssp. *mexicana* is more closely allied to ssp. *acuta* than to ssp. *hartwegii*. Subspecies *hartwegii* has flowers that are very similar to those of ssp. *wrightii*, but differs in habit and range. Wettstein's *Gentiana mexicana hartwegii* forma *pringlei* is a high-altitude form, but in some duplicates of the Pringle type collection the plants are as large as the so-called "low-elevation" form. With the little material available it would be futile to segregate smaller plants of higher elevations. My own field experience with other species is that in the plants of a continuous population reduction in size regularly occurs at higher altitudes.

12. *GENTIANELLA auriculata* (Pall.) J. M. Gillett, comb. nov.*Gentiana auriculata* Pallas, Fl. Ross. 1<sup>2</sup>:102, t. 92, f. 1. 1788, ex char. & ic.*Dasystephana auriculata* (Pall.) Borckh. in Roem. Archiv f. Bot. 1<sup>1</sup>:26. 1796.*Hippion auriculatum* (Pall.) Schmidt, in Roem. loc. cit. 11. 1796.*Amarella auriculata* (Pall.) Greene, Leaf. Bot. Obs. & Crit. 1:53. 1904.

Caulescent annuals (?), 2–25 cm. tall, simple or branched, occasionally from the base, more frequently above. Basal leaves forming loose rosettes, obovate-spatulate to elliptic, the apex rounded or obtuse, the base attenuate, 4–30 mm. long, 1–13 mm. wide; median and upper leaves elliptic-ovate to broadly ovate, obtuse to rounded, the base broadened and clasping, 8–40 mm. long, 3–15 mm. wide; the upper leaves very slightly smaller or equal to the median. Flowers axillary or terminal, in simple or aggregate cymes or occasionally solitary, the terminal flower conspicuously larger than the lateral, the terminal pedicels extremely variable, subsessile to 3.5 cm. long, the lateral equal to or correspondingly shorter than the terminal. Calyx 7–9 mm. long, 4- to 5-lobed (4-lobed in North America), the tube about 6 mm. long; lobes about equal, or either the inner or the outer pair broader than the others, strongly and reticulately veined, broader than long, about one-third the length of the tube, the margins entire or minutely papillose, the base auriculate. Corolla blue, narrowly funnelform to salverform when the lobes are fully expanded, 18–28 mm. long, 5–8 mm. wide at the orifice; lobes ovate,  $\frac{1}{4}$ – $\frac{1}{3}$  the length of the tube, the tips obtuse to subacute, the sinuses acute and frequently concealed by the imbrication of the lobes, the tube provided with a faucal corona, the fimbriae united at the base to form a lacerate squamella extending across the base of each lobe; interstaminal glands inconspicuous and extremely small, scuti-form, at the very base of the corolla tube. Stamens slightly exserted; filaments inserted about the middle of the corolla tube, the wings about 1 mm. wide at the base, tapering gradually above; anthers oblong, 1.6–1.8 mm. long, about 1 mm. wide, versatile and attached near the middle. Pistil sessile, the ovary cylindrical, 15 mm. long, 1.5 mm. wide, tapering slightly near the tip; stigma sessile, oblong, 1.5 mm. long, 1.0 mm. wide, erect. Capsule slightly longer than the marcescent corolla, about 25 mm. long, dehiscent at the tip; seeds approximately ovoid, 0.75 mm. long, 0.6 mm. wide, smooth, minutely wrinkled under magnification, light brown.

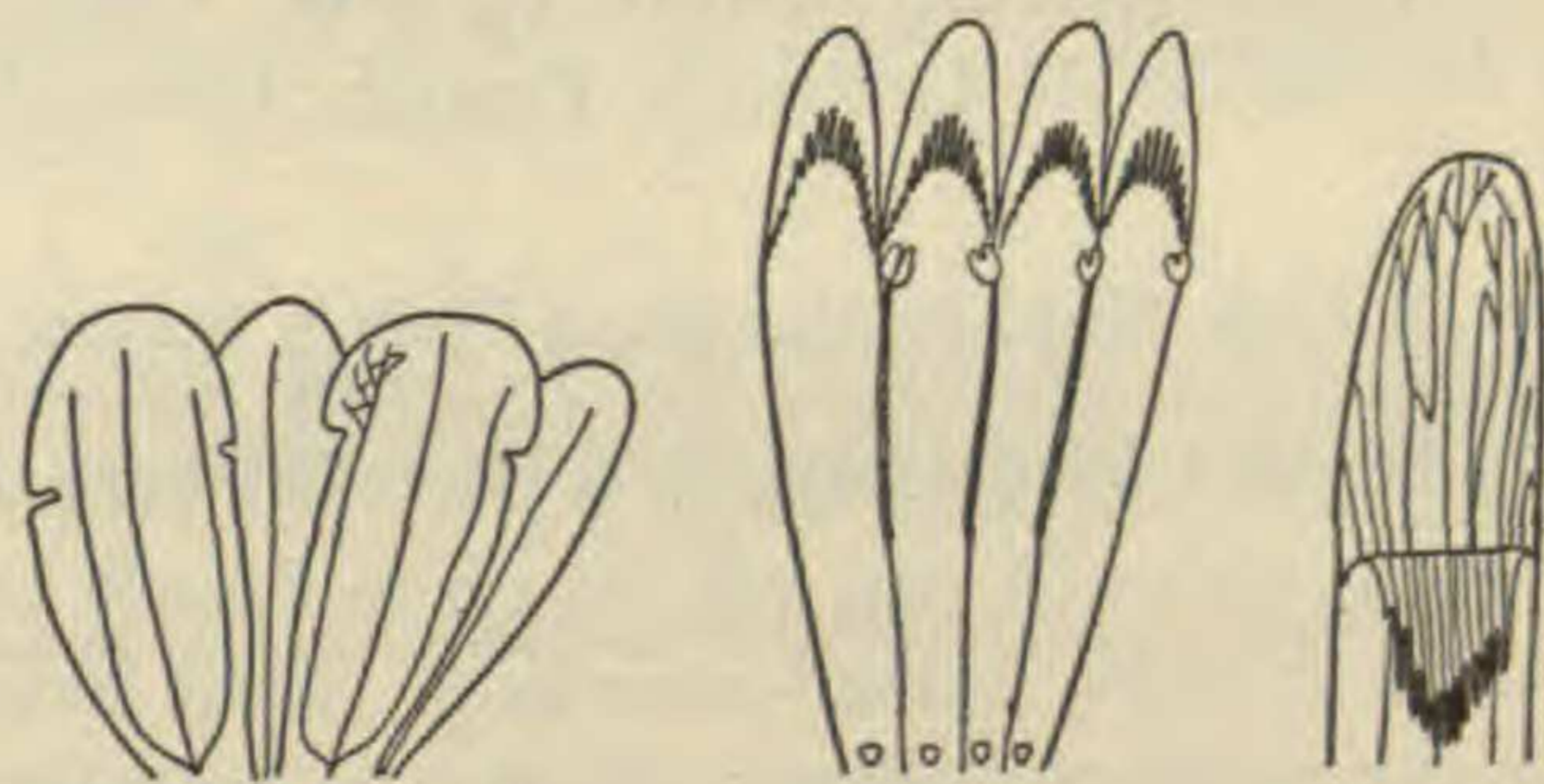


Fig. 8. Calyx ( $\times 2$ ), corolla ( $\times 1$ ), and corolla lobe of *Gentianella auriculata*.

On Attu Island, at the western extremity of the Aleutian Islands, on the Commander Islands in Behring Sea, in Kamchatka, on the islands north of Japan and about the Okhotsk Sea; on gravelly slopes at altitudes from sea level to 300 meters; flowering throughout August and presumably well into September; fruiting in September. Further habitat data are lacking since all Asiatic material examined gives no other information than the approximate location of the collection.

ALASKA: Aleutian Islands, Attu Island, vicinity of Massacre Bay, Lookout Hill, *Van Schaack* 66 (MO, US), 748 (MO), 929 (MO, US).

The description has been based primarily on Kamchatkan and Japanese material since so little is available from North America. The excellent material from Attu Island collected by Van Schaack constitutes the only record of this plant from this continent. This fact has already been pointed out by Hultén in his flora. On a field label, Van Schaack notes that the specimens are 4-merous, while the material from Kamchatka and the Commander Islands is 5-merous. However, examination of more material shows that 4- and 5-merous material occurs both in Kamchatka and in the Commander Islands (Bering Island). As seen in other species the number of corolla or calyx lobes is a variable character, both types commonly occurring even on the same plant; indeed, in *G. aurea* and *G. amarella* ssp. *acuta* a 5-lobed calyx is frequently associated with a 4-lobed corolla.

### SUBGENUS III. COMASTOMA (Wettst.) J. M. Gillett, stat. nov.

*Gentiana* sect. COMASTOMA Wettst. in Oesterr. Bot. Zeitschr. 45:174. 1896.

*Lomatogonium* A. Br. sect. COMASTOMA (Wettst.) Löve & Löve, in Acta Hort. Goto-  
burg. 20<sup>4</sup>:117. 1956.

Flowers 4- to 5-merous. Calyx tube short, the lobes foliaceous, sinuses lacking an inner membrane. Corolla 4- to 5-parted, the lobes ovate, entire, the orifice with two evascular fimbriate scales at the base of each lobe, the interstaminal glands epipetalous and in pairs. Stamens inserted slightly above the middle of the corolla tube, the anthers oblong, slightly longer than wide, the filaments minutely papillose. Ovary with several rows of ovules that frequently extend nearly to the center of the carpel wall. Seeds ovoid, somewhat flattened, smooth or slightly papillose at one end.

13. GENTIANELLA TENELLA (Rottb.) Börner, Fl. deut. Volk, 542. 1912. (*G. tenella* (Rottb.) H. Sm. ex Hylander, in Uppsala Univ. Arssk. 259. 1945, superfluous comb.)

*Gentiana tenella* Rottb. in Kiob. Selsk. Skrift. (Acta Hafn.) 10:436. 1770. (T.: Col-  
lector unknown, C!)

*Lomatogonium tenellum* (Rottb.) Löve & Löve, Acta Hort. Gotoburg. 20<sup>4</sup>:117. 1956.

Annuals 1-26 (usually about 6) cm. tall, loosely to densely caespitose or branching above, or simple, the branches curved-ascending. Basal leaves two or forming dense rosettes, frequently deciduous, elliptic, obovate to spatulate, 3-10 mm. long, 1-4 mm. wide, the apex rounded to obtuse, attenuate to the base; median and upper leaves ovate to ovate-elliptic, 4-9 mm. long, 1-3 mm. wide, the apex obtuse,

the base attenuate, somewhat clasping. Flowers solitary, terminal or axillary. Pedicels 2–10 cm. long. Calyx 4- to 5-merous, the tube nearly obsolete, 5–10 mm. long, the outer lobes foliaceous, broadly ovate to lanceolate, obtuse to acuminate, about 10 mm. long, 2–7 mm. wide, with or without an outer inflated saccate protrusion at the base, the inner lobes lanceolate, slightly shorter than the outer and about half to one-third as wide, the margins entire, the sinuses concealed by the imbrication of the lobes. Corolla blue to white, tubular to somewhat salverform, about 11 mm. long, 2–3 mm. wide at the orifice, the lobes oblong-ovate, imbricate, one-third to half as long as the tube, the tips obtuse, the orifice bearing at the base of the corolla lobe two groups of 4–6 blunt evascular fimbriae united at the base to form two fimbriate scales, or nearly free about half the length of the lobes, the interstaminal glands indistinct, appearing by transmitted light as two greenish, oblong stains about 1 mm. above the base of the tube. Stamens included, the filaments inserted near the upper third of the corolla tube, the wings about 0.3–0.4 mm. wide at the base, slightly tapering towards the anthers, the margins minutely papillose; anthers oval, about 1 mm. long, 0.5 mm. wide, versatile and attached near the middle. Pistil sessile; ovary fusiform, about 5 mm. long, about 1.5 mm. wide; stigmas sessile, ovate-oblong, 0.5 mm. long and wide, erect, the stigmatic surfaces facing inwards, recurving in fruit. Capsule longer than the marcescent corolla, up to 12 mm. long, dehiscent at the tip, the valves recurving about half their length. Seeds ovoid, slightly flattened, 0.75 mm. long, 0.5 mm. wide, the surface smooth, sub-papillose to papillose at one end, light brown.

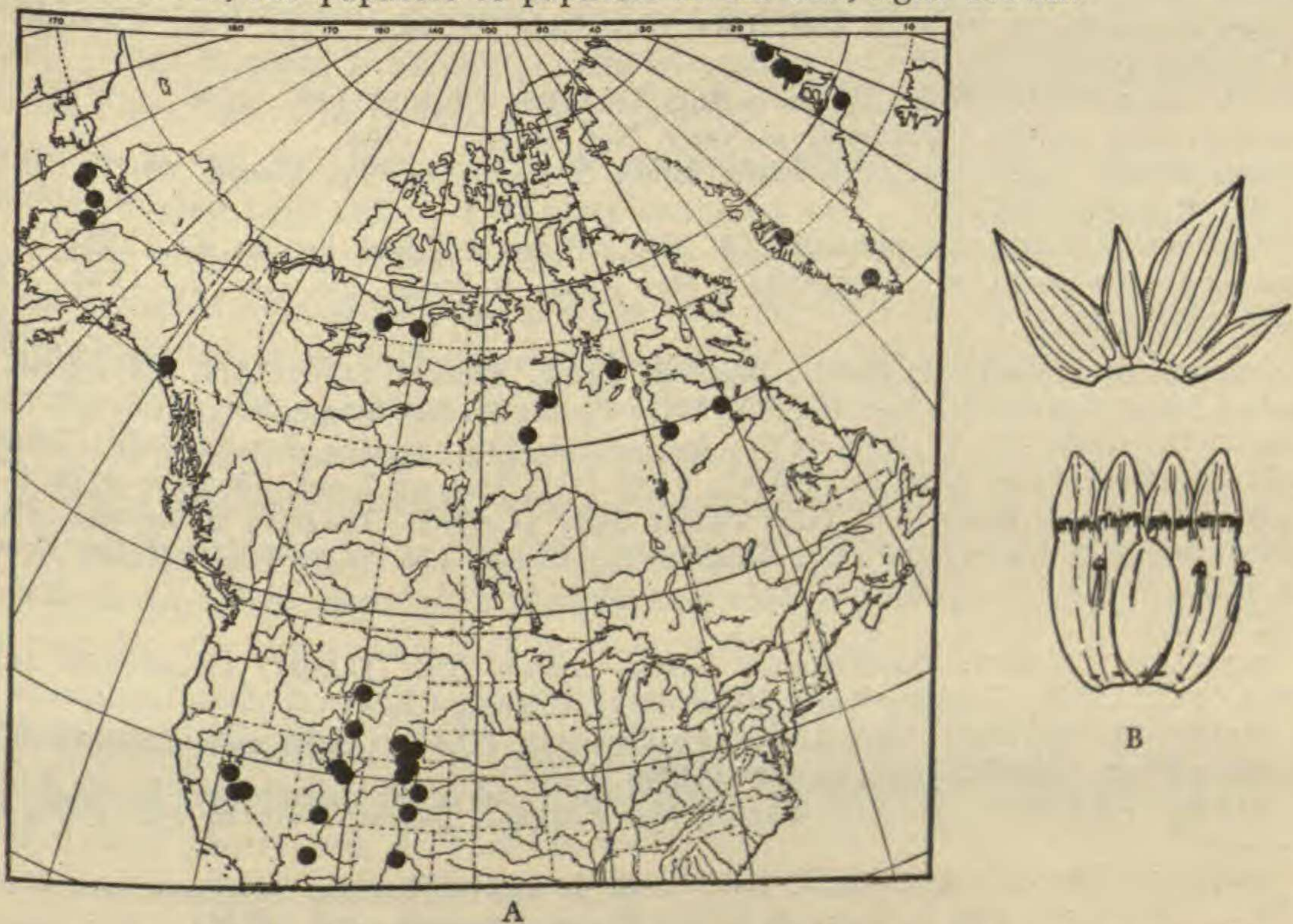


Fig. 9. A, distribution of *Gentianella tenella* in North America. B, calyx and corolla of *G. tenella*,  $\times 1\frac{3}{4}$ .

*Gentianella tenella* occurs in northern Europe and Asia and in the mountains of the southern parts of those continents. In North America the species occurs in Greenland, northern continental Canada and Alaska; in the Rocky Mountains as far south as Arizona and New Mexico and in Mono County, California. Because the plants are small and inconspicuous they are often overlooked by collectors. This may explain the scattered distribution pattern. *G. tenella* grows in a variety of habitats from sandy sea beaches, moist and dry slopes, lake margins, wet meadows, rocky places, to alpine tundra, at altitudes from a few feet above sea level in the northern part of the continent to 3500 meters in the southern part; flowering from late July until late August or early September regardless of latitude; fruiting from late August until September.

## KEY TO THE SUBSPECIES

- a. Calyx lobes ovate to lanceolate; branches few; cauline leaves with evident internodes.....  
 .....13a. *G. tenella* ssp. *tenella*  
 aa. One or two calyx lobes broadly ovate; branches numerous; stem leaves compacted by a shortening of the lower internodes. Pribilof Islands, Alaska.....13b. *G. tenella* ssp. *pribilofii*

## 13a. GENTIANELLA TENELLA (Rottb.) Börner, ssp. TENELLA

*Gentiana koeningii* Gunner, Fl. Norv. 2:102. 1772, ex char.

*Gentiana glacialis* Thom. ex Vill. Hist. Fl. Dauph. 2:532. 1787, ex char. (T.: Hall 652)

*Gentiana tetragona* Roth, Tent. Fl. Germ. 2:290. 1789, ex char.

*Hippion longepedunculatum* Schmidt, in Roem. Archiv f. Bot. 1:21. 1796, ex char.

*Gentiana borealis* Bunge, in Nouv. Mem. Soc. Nat. Mosc. 1:251. t. 10. f. 2. 1829, ex ic.

*Cicendia tenella* (Rottb.) Raf. ex Jacks. Ind. Kew. 1:533. 1893.

*Gentiana monantha* A. Nels. in Bull. Torr. Bot. Club 31:244. 1904. (T.: Clements & Clements 456!)

*Amarella monantha* (A. Nels.) Rydb. in Bull. Torr. Bot. Club 33:148. 1906.

*Amarella tenella* (Rottb.) Cockerell, in Amer. Nat. 40:871. 1906.

*Gentiana tenella* Rottb. var. *occidentalis* Rouss. & Raym. in Nat. Canad. 79:77. 1952. (T.: Rousseau 200!)

*Gentiana tenella* Rottb. var. *monantha* (A. Nels.) Rouss. & Raym. loc. cit. 77. 1952.

*Gentiana tenella* Rottb. var. *monantha* f. *alba* Rouss. & Raym. loc. cit. 79. 1952. (T.: Duran 3105!)

GREENLAND: Manby Peninsula, Blossville Coast, *Bartlett 311* (CAN, US); head of Muskox Fjord, *Seidenfaden 309* (C, NY, US); Geologfjorden, Stromdbergs Halvö, *Seidenfaden* & *Ostenfeld 369* (C, GH, NY); Julianehaab, Dist. Igaliko, *Porsild 8086* (CAN); Traill Island, *Sörensen 3274* (C, CAN), *3276* (C); Hudson Land, *Sörensen 5032* (C); Sondre Stromfjord, *Jensen s. n.* (C); *Porsild 8545* (CAN). Location unknown: *Elvin, Hartz s. n.* (C), *Jensen s. n.* (C), *Sabanse* (?), *Kruuse s. n.* (C); Hurry Inlet, *Kruuse s. n.* (C).

## CANADA:

KEEWATIN DISTRICT: Southampton Island, *Brown 608* (DAO); Chesterfield Inlet, *Savile 1391* (DAO); Esquimo Point, *Marsh 62* (UT, photo CAN).

MACKENZIE DISTRICT: Coppermine, *Findlay 242* (DAO); west side Bathurst Inlet, Burnside River, *Kelsall* & *McEwan 182* (CAN).

YUKON TERRITORY: St. Elias Range, Mt. Turquat, *Bakewell 80*, & *150* (GH, fide Porsild).<sup>61</sup>

QUEBEC: Poste de Povugnituq, rive est de la baie d'Hudson, *Rousseau 140*, & *200* (JBM); Baie Kayak dans l'estuaire de la baie Payne, *Rousseau 1496* (JBM).

<sup>61</sup> Porsild, in Nat. Mus. Can. Bull. 121:275. 1951.

## UNITED STATES:

ALASKA: Nome, Seward Peninsula, *Scamman 3910* (GH), *Thornton 439* (US); Port Clarence, Teller, *Porsild & Porsild 1488* (CAN, GH); Unalaklet, *Porsild & Porsild s. n.* (CAN, GH, US); Kotzebue Sound, *Eschscholtz s. n.* (US); Kotzebue, *Lepage 25404* (CAN, DAO), *Scamman 4064* (GH).

ARIZONA: Coconino Co.: San Francisco Mts., *Knowlton 131* (US).

CALIFORNIA: Mono Co.: Bloody Cañon (Mono Pass), *Congdon Herb.* (GH); White Mts., McAfee Meadow, *Duran 2816* (F, GH, MO, NY, US).

COLORADO: Clear Creek Co.: near Empire, *Patterson 245* (C, GH, MO, NY, US). Clear Creek-Summit Cos.: Mount Flora, *Parry s. n.* (GH, MO, US); Gray's Peak, *Patterson s. n.* (MO, US), *Patterson & Beatty s. n.* (F, US). Gilpin Co.: James Peak, *Cox 233* (F, MO), *Fuller s. n.* (MO). Grand Co.: Lulu Pass, *Clokey et al. 4239* (NY, US, WS). Larimer Co.: Long's Peak, *Holm s. n.* (MO). Saguache Co.: Cristones, Sangre de Cristo Range, *Brandegge s. n.* (MO). San Miguel Co.: Trout Lake, *Payson & Payson 4199* (GH, MO). Location unknown: Bear Creek, *Purpus 700* (F); Mirror Lake, *Clements & Clements 456* (C, GH, MO, NY, RM, US).

NEVADA: Esmeralda Co.: White Mts., *Duran 3105* (F, GH, JBM, MO, US).

NEW MEXICO: Santa Fe Co.: vic. Santa Fe, *Arsène & Benedict 16099* (F, US).

UTAH: Duchesne Co.: Mt. Emmons, *Hermann 5201* (GH, MO); Garfield Co.: Aquarius Plateau, *Dixon s. n.* (F), *Ward 623* (GH, MO, US). Summit Co.: Lamotte Peak, *Hermann 5973* (MO); lower Henry Fork Basin, *Maguire et al. 14451, 14619* (WS).

WYOMING: Albany Co.: Medicine Bow Mts., *Ownbey 176* (WS). Park Co.: Bear-tooth Mts., *Williams & Williams 3762* (GH, MO, NY). Sublette Co.: Wind River Mts., *Nuttall s. n.* (GH); Yellowstone Park, Lone Star, *Reynolds 74* (F).

The degree of variation in this species is quite as high as in the other species of the genus. While I have not seen the type of Thomas' *Gentiana glacialis*, I have seen a sheet from the Copenhagen collection labeled on the back in the lower left-hand corner, "*Gentiana glacialis*", and in the lower right-hand corner, "dedit Villars." This material is certainly authentic, and may even be an isotype. Villars, in his *Flora*, refers to Gmelin's 'Flora Sibirica': "Elle paroît gravée dans Gmelin Tab. 51. B. vol. IV. sous le nom de *gentiana pumila centaurii minoris folio flore piloso*. Stelleri pag. 105." This plate compares very closely with the Copenhagen specimen with the exception of the corolla, which is pictured as having five lobes. This feature is not critical, however, as such variation in lobe number is common throughout the genus with the exception of the fringed gentians where four parts are the rule. On the other hand, the five lobes may have been an error by the artist, for in all other respects the illustration is *G. tenella*.

Nelson described *Gentiana monantha* partially because he thought that the true *G. tenella* Rottb. was an arctic plant with 5-merous flowers: "The true *G. tenella* Rottb. is an arctic plant with 5-merous flowers, the obtuse corolla lobes as long as its tube; the calyx only half as long as the corolla and with unequal sepals." The original description of *G. tenella*, however, states: "fauce 4fida, barbata", and "Perianthium 4phyllum".

A small population from St. Paul Island, Pribilof Islands, Alaska, consists of rather short plants with a dense cluster of ascending branches. Both the 4- and 5-merous condition occurs and one or two calyx lobes are more broadly ovate than usual. This population may be referred to:

13b. *GENTIANELLA TENELLA* (Rottb.) Börner, ssp. *pribilofii* J. M. Gillett, sub-spec. nov.

Plantae 3–5 (–8) cm. altae; folia caulinarum plerumque in rosula per contractionem internodiorum inferiorum; ramis numerosis ascendentibus. Flores (4)–5-meri; calycis lobis exterioribus tum 1 tum 2 latius ovatis.

ALASKA: Pribilof Islands: Seal Island, *Bryant s. n.* (US); St. Paul Island, *Elliott s. n.* (GH, US), *Kincaid s. n.* (CAN, C, NY); St. Paul Island, Behring Sea, in 1891, *J. M. Macoun* (CAN HOLOTYPE, GH, MO, NY), in 1896 (CAN, US), in 1892 (CAN, US), in 1914 (CAN, GH, NY, US), *White s. n.* (GH, NY), *Whitney s. n.* (US).

### ENUMERATION OF THE SPECIES

#### Subgenus I. EUBLEPHIS

1. *G. detonsa* (Rottb.) G. Don
  - a. ssp. *detonsa*
  - b. ssp. *yukonensis* J. M. Gillett
  - c. ssp. *nesophila* (Th. Holm) J. M. Gillett
  - d. ssp. *raupii* (Porsild) J. M. Gillett
  - e. ssp. *elegans* (A. Nels.) J. M. Gillett
  - f. ssp. *superba* (Greene) J. M. Gillett
  - g. ssp. *lanceolata* (Benth.) J. M. Gillett
  - h. ssp. *holopetala* (A. Gray) J. M. Gillett
2. *G. crinita* (Froel.) G. Don
  - a. ssp. *crinita*
  - b. ssp. *procera* (Th. Holm) J. M. Gillett
  - c. ssp. *victorinii* (Fern.) J. M. Gillett
  - d. ssp. *macounii* (Th. Holm) J. M. Gillett
3. *G. barbellata* (Engelm.) J. M. Gillett
4. *G. simplex* (A. Gray) J. M. Gillett

#### Subgenus II. GENTIANELLA

##### Sect. AMARELLA

##### Ser. I. ARCTOPHILAE

5. *G. wislizeni* (Engelm.) J. M. Gillett

6. *G. propinqua* (Richards.) J. M. Gillett
  - a. ssp. *propinqua*  
forma *acyanea* J. M. Gillett
  - b. ssp. *aleutica* (Cham. & Schlecht.) J. M. Gillett
7. *G. aurea* (L.) H. Sm. ex Hylander
8. *G. quinquefolia* (L.) Small
  - a. ssp. *quinquefolia*
  - b. ssp. *occidentalis* (A. Gray) J. M. Gillett
9. *G. microcalyx* (Lemmon) J. M. Gillett

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11. *G. amarella* (L.) Börner
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  - b. ssp. *acuta* (Michx.) J. M. Gillett
  - c. ssp. *mexicana* (Griseb.) J. M. Gillett
  - d. ssp. *sandiana* J. M. Gillett
  - e. ssp. *wrightii* (A. Gray) J. M. Gillett
  - f. ssp. *hartwegii* J. M. Gillett
12. *G. auriculata* (Pall.) J. M. Gillett

##### Subgenus III. COMASTOMA

13. *G. tenella* (Rottb.) Börner
  - a. ssp. *tenella*
  - b. ssp. *pribilofii* J. M. Gillett



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